

**EFFECTS OF CYCLONES ON TROPICAL RAIN FOREST
STRUCTURE AND DYNAMICS**

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Say: "If the sea were ink for the Words of my Lord, surely, the sea would be exhausted before the Words of my Lord would be finished, even if We brought like it for its aid."

(The Quran, 18:109)

Abstract

Spatial patterns of forest trees, stand level effects of cyclones, and factors affecting mortality and growth of individual trees were investigated in 20 experimental plots (0.5 ha) in North Queensland tropical rain forests, Australia. Cyclone disturbance has been recorded in individual plots for 20 times since establishment in 1971. Spatial point patterns of trees were mapped, and pair correlation and mark correlation function were used to investigate relationships between the trees. Effects of cyclones on stand level properties of the forests (total basal area, stem densities, stem size inequality, species diversity, recruitment, mortality) were estimated using generalised additive modelling. Factors affecting individual tree mortality and growth were analysed in generalised mixed effects modelling. The spatial pattern analysis showed minor changes of tree density and tree death in the forest spatial patterns following cyclones. The models revealed that the forest properties were changed significantly. Cyclones decreasing total basal area and increased tree mortality rates and number of abundant species. Higher mortality rates are likely influenced by individual tree characteristics of low wood density, negative growth rates and belonging to particular sets of families. Factors that increase growth rates are include higher crowding effects of tree density, cyclone occurrence, crowding effects by smaller trees, and trees of some families. Slower growth rates are likely influenced by higher wood density, higher surrounding basal area of competing trees and in certain families. From this research, evidence has found for cyclones to be a factor increasing stand level mortality rates but not individual tree mortality. The dynamics from individual trees in mortality and growth, forest spatial patterns and stand level properties has characterised the tropical rain forests of North Queensland in facing frequent cyclone disturbances.

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1 INTRODUCTION

1.1 General introduction

Tropical rain forests are widely accepted to have the greatest species richness of any biome, and they therefore provide a wide range of possibilities for ecological studies. Research has shown how dynamics and interactions in the forests determine changes in the structure, composition and function of the forest (Ghazoul and Sheil 2010). Forests can be characterised by internal spatial patterns of the trees and a spatial lattice of various species, sizes and wood densities. These vary in their rates of growth and mortality, as well as in their interactions (Dale 1999, Turner 2001).

Forest dynamics include natural and anthropogenic disturbances (Ghazoul and Sheil 2010) which could influence the responses of forest structure (Goldammer 1992). To investigate such responses towards disturbances, it is necessary to analyse the spatial patterns of the trees. There are a large number of forest spatial pattern studies (Goreaud et al. 1997, Condit et al. 2000, Plotkin et al. 2002, Wiegand et al. 2007, Sungpalee et al. 2009) with most concerning general species composition and functions (i.e., distribution, dispersal) of the forest trees. However, little research into forest disturbances has been conducted based on spatial structures. Consequently, the spatial organisation of forests is still poorly understood, although it may be an important factor in forest stability in facing the disturbance.

Spatial pattern analysis has been applied in many fields including astronomy, geology, archaeology and material science; further, it has been intensively applied in tropical ecology (Condit et al. 2000, Stoyan and Penttinen 2000). A system is generally considered to have spatial properties if data observations exist in absolute locations or relative positions. Such

analysis can allow researchers to study the influence of ecological processes and environmental conditions on species distribution, for example by addressing the position and size of individuals of different species (Batista and Maguire 1998, Plotkin et al. 2002, Getzin et al. 2011, Ledo et al. 2011). Studies of forests have looked at tree spacing and patterns (Batista and Maguire 1998, Getzin et al. 2011), species behaviour (Keppel et al. 2010), forest structure (Goreaud et al. 1997, Batista and Maguire 1998, Murrell 2010) and mortality (Baker et al. 2005, Jonsson et al. 2007, Suzuki et al. 2008). For tropical forests, the most common approach is to investigate the distribution of different tree species within plots (Condit et al. 2000, Condit et al. 2006).

Forests facing frequent cyclones have been broadly studied, but these investigations commonly emphasised one specific cyclone event. Very few studies have considered series of cyclones or have adopted spatial pattern analysis to determine the effects of cyclone on forest trees. Commonly, studies on cyclones' impact on forests describe either the long term or immediate effects. While some studies have been done on forests that have experienced a series of frequent cyclones, for instance the tropical forests of North Queensland, none has assessed the direct effects of every cyclone over a longer period. Such study would be of great interest, because cyclones may contribute towards shaping the pattern of tropical rain forests. Therefore, this study aimed to understand how cyclones influence the spatial structure of forests, in particular of the direct effects of cyclones at forest stand level, as well as in terms of the physical properties of individual trees.

This study analysed the effects of cyclones using long term survey data obtained from a project established and supported by the Commonwealth Scientific and Industrial Research Organisation (CSIRO) and the Australian Cooperative Research Centres (CRC). The project is known as The CSIRO Rainforest Permanent Plots of North Queensland, Australia. The dataset has been recorded since 1971, and covers a period with 20 cyclone occurrences

faced by the forest plots. Analyses involved determining the spatial patterns and stand level effects of cyclones on forest plots, as well as their effects on mortality rates and the growth rates based on stand level and individual trees.

1.2 Spatial point pattern analysis

Dale (1999) described how spatial patterns can be used to test hypotheses. The idea of deriving information from spatial patterns started with Watt (1947), who believed that individuals that form patterns can be used to understand how a plant community assembles and functions. The theory of spatial patterns then developed from many spatial studies including on interspecific association in the 1950s and 1960s (Perry et al. 2006, Gotzenberger et al. 2012) and 'assembly rules' (Gotzenberger et al. 2012) in the 1970s.

Investigating spatial patterns always begins with descriptive analyses of point patterns in space where they may be described as being clumped, clustered, regularly arranged or randomly distributed (Dale 1999). Natural patterns of trees often show clumping or clustering especially during sapling stage, as a result of seed dispersion. The trees become more regularly distributed as they grow older. For trees in tropical rain forests, such spatial patterns exist on various scales or there may also be combinations of patterns. Point pattern is actually a realisation of a process, where points are some set of coordinates with each point considered as an event which is termed a 'marked' pattern (Perry et al. 2006). Thus for example, the marks may be characterised by the size, species or wood density of the trees. The corresponding marked spatial point pattern is an important source of information because the points themselves and changes in their pattern are highly indicative of certain processes (Stoyan and Penttinen 2000).

The advent of computer technologies did much to enhance the insights that can be gained from spatial pattern analysis. The recent computer development with powerful calculations has brought many benefits to the process of spatial pattern analysis. In particular, complex relationships can be rapidly visualised and complex spatial patterns can be accurately modelled. Forest structures are complex, as both horizontal and vertical space is used by trees, but point pattern analysis can simplify this complexity by mapping the exact location of each tree into horizontal space only.

Common techniques for spatial pattern analysis include Kernel Density Estimation (Ripley's K-function) and associated tests. Ripley's K-function (Ripley 1977, Batista and Maguire 1998) can be used to assess the distribution of points by calculating the number of points per unit area, termed the intensity (λ) at different scales (Goreaud et al. 1997, Batista and Maguire 1998). The pair correlation function is a common test derived from the Ripley's K, normally carried out to understand relationships between two points. More sophisticated analysis of point patterns incorporates techniques for handling the spatial correlation of marked points and edge-correction for points close to the border (Goreaud et al. 1997, Batista and Maguire 1998, Perry et al. 2006). There are many other approaches developed of various levels of usefulness (Perry et al. 2006) in the field of ecological diversity.

The mark correlation function has received considerable research attention as a technique for handling spatial correlations (Dale 1999, Suzuki et al. 2008, Walder and Walder 2008, Ledo et al. 2011). The ecological application of this technique has included the analysis of tree spatial patterns in many studies. For example, it has been used to determine hierarchy of tree sizes (Suzuki et al. 2008) and the relative biomass (Law et al. 2009) of each individual trees in a spatial pattern. Furthermore, the approach can be used to describe quantitative relationships between marked points (Law et al. 2009) or to measure a process that involves two types of points. As a result, this function is able to identify relationships

between points (Stoyan and Penttinen 2000). The research describes in the present thesis used mark correlation functions in which the points were the positions of forest trees, and the mark characteristics were either categorical such as live or dead tree, or continuous, such as basal area size and biomass.

1.3 Factors that drive spatial patterns in tropical rain forest

There are many fundamental ecological processes that can give rise to spatial patterns within forests (Figure 1.1). The spatial patterns of tropical rain forests can be summarised as resulting from both endogenous (e.g. species diversity, population intensity) and exogenous factors (e.g. disturbance, soils, slopes) (Murrell 2010).

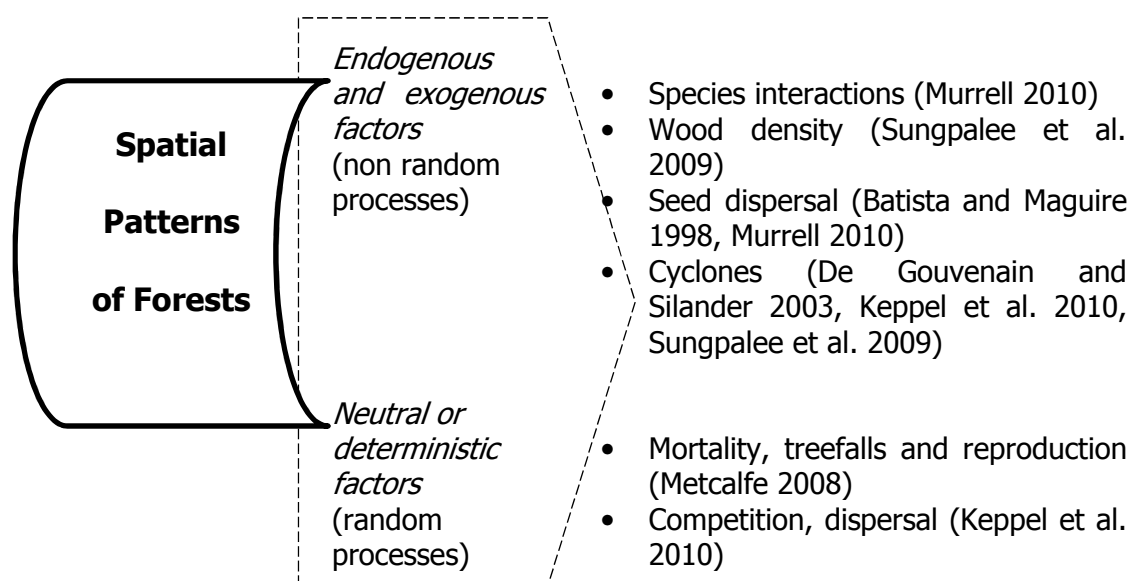


Figure 1.1 Factors that may influence spatial patterns within forests

Spatial forest structures were defined by Murrell (2010) as the spatial arrangement of individuals, which might be due to random and non-random processes (Batista and Maguire 1998, Wolf 2005). A random distribution of trees could be due factors such as competition and predation. Non-random processes also influence the spatial structure of forests. Examples of non-random processes (Batista and Maguire 1998) include tree establishment after clear cut and tree establishment under the canopy. Alternatively, other studies consider

the spatial structure of forests as the result of neutral and deterministic factors. For instance, Keppel et.al. (2010) included among 'neutral' factors dispersal limitation and stochastic events, while deterministic factors were said to be the same as habitat factors.

1.3.1 Cyclone disturbance

Cyclone or hurricane-perturbed forests are found in the tropical regions of African and Australia (De Gouvenain and Silander 2003), New Guinea (Keppel et al. 2010), as well as in many scattered locations of American rain forests (De Gouvenain and Silander 2003, Lugo 2008). Climate change may increase the intensity of cyclones, and this could have major consequences for the structure, composition, and dynamics of forests (De Gouvenain and Silander 2003).

Large works has been done for studying hurricane or cyclone (hurricane is term used in the Atlantic and Pacific, cyclone is in the tropics), generally on ecological effects of cyclone on the forest trees, cyclone-fire combination, as well as anthropogenic effects. The present study highlights the ecological effects of the cyclone. Cyclones could affect tree density, canopy structure and even the topographic location of trees. Lugo (2008) suggested six ecological role of cyclones, where four of them are can be considered related to spatial character of the forest trees: 1. Change available ecological space to organisms; 2. Increase the heterogeneity of the forest landscape and the variability in ecosystem processes; 3. Rejuvenate the landscape and its ecosystem through succession; 4. They shape the structure, species composition and diversity.

The Puerto Rico and Caribbean tropical forests have been widely documented for the effects of hurricanes (Lugo 2008) on their structure, composition and dynamics (Boose et al. 1994, Foster et al. 1999). For instance in Puerto Rico, hurricanes had dramatically changed

vegetation cover and distribution of the forests (Foster et al. 1999) which were believe related to factors like the high frequency of hurricane, topographic exposure to the wind, elevation of the forests (Foster et al. 1999), soil conditions and attributes of individual trees (Canham et al. 2010).

Bellingham (2008) reviewed cyclones affecting Australian rain forests. The effects of cyclones were classified as immediate effects, effects of single cyclones, effects of multiple cyclones, interactions with other disturbances; more advanced studies had sought to predict how future cyclones could affect forest composition. He concluded that rain forests in some coastal areas with abundant lianas were hyperdisturbed had uneven canopies; different responses were found between species in term of mortality, recruitment and growth. The overall and effects of cyclones on species diversity were related to their frequency in the area, the strength of those cyclones, and the interval between the last cyclone and the study. Nonetheless, none of these studies seems to have measured the direct effects of a cyclone using a long term forest survey with repeated cyclone events as in the tropical rain forests of North Queensland.

In Queensland, Australia, De Gouvenain and Silander (2003) showed that frequent cyclones resulted in lower canopies and higher tree densities; but was found not significant for American rain forests. Keppel et al. (2010) found that cyclone frequency appears to affect community assembly in lowland rain forest more than other areas. Cyclone were also found to cause changes in the canopy cover (Staben and Evans 2008), to damage individual trees (Cook and Goyens 2008, Metcalfe et al. 2008) and to affect the species composition in particular localities (Metcalfe et al. 2008).

The forests of North Queensland have frequently experienced cyclones, and this is likely to have affected the structure of those forests. The dataset used in the present study contains

coordinates for each tree, diameter at breast height, live/dead status, taxonomy and wood density, as well as cyclone history. This makes the dataset ideal for the purpose of understanding the effects of cyclones. In this research, the frequency of cyclones in the study area are related to the forest structures, by investigating tree spatial patterns and modelling the effects of cyclones on the forests.

1.3.2 Wood density

Wood density is thought to be a major factor in tree response to cyclones (De Gouvenain and Silander 2003, Metcalfe and Bradford 2008, Metcalfe et al. 2008, Keppel et al. 2010). High wood density is usually described as a benefit, as it makes stem breakage less likely and is more resistant to decay. Generally, higher wood density decreases both growth rates and mortality rates, as found in many studies in the Amazon (Chao et al. 2008), Panama (Muller-Landau 2004) and Thailand (Sungpalee et al. 2009).

Trees with higher wood density might be favoured on slopes that face strong and frequent winds (Sungpalee et al. 2009) or in areas that frequently face cyclone disturbance (De Gouvenain and Silander 2003, Keppel et al. 2010). But the size of the trees may play a role too; Chao et al. (2008) found that large trees of high wood density had a higher probability of death. However, lower wood density can confer advantages in terms of stem elasticity (Larjavaara and Muller-Landau 2010) which would be especially important in the face of cyclonic winds.

Even so, Larjavaara and Muller-Landau (2010) explain that a thicker trunk of lower wood density may be less flexible than a thinner trunk of higher wood density, and trees with high flexibility are likely to be more resistant to high wind.

1.3.3 Tree mortality

Metcalfe and Bradford (2008) found in Queensland, Australia that larger trees were more likely to die than small trees when damaged by wind, whereas smaller trees were more likely to recover (Metcalfe and Bradford 2008). This means that species and size should be considered when accounting for tree mortality especially following cyclone events.

Tree mortality depends on individual factors of the tree, such as age, size, growth rate and crown size (Batista and Maguire 1998, Lin et al. 2004, Chao et al. 2008). Many studies have analysed the spatial attributes of individual trees to account for mortality patterns over years (Goreaud et al. 1997, Condit et al. 2000, Condit et al. 2006, Muller-Landau et al. 2006, Coomes and Allen 2007b, Chao et al. 2008, Metcalfe and Bradford 2008, Law et al. 2009, Sungpalee et al. 2009, Getzin et al. 2011, Webb et al. 2011). But to understand what factors affect these mortality patterns, the analysis has to involve both individual tree attributes and stand level factors.

1.3.4 Interactions between trees

In forest with a mixture of tree species, key question is why tree species are spatially clumped rather than more evenly distributed (Plotkin et al. 2002). Most trees are aggregated with conspecific individuals, instead of being randomly distributed. This is especially true of the smaller trees (1-10 cm diameter at breast height; dbh); while larger trees (≥ 10 cm dbh) show similar pattern, it is weaker (Condit et al. 2000). This may be due to herbivores and plant diseases reducing the aggregation of the smaller (and therefore younger) trees.

The individual spacing of trees needs to be considered when assessing the spatial pattern of a forest. The dispersal of seeds is important in driving the interactions between trees. A

lesser degree of dispersal often causes species to occur in approximately circular clumps which do not correspond to the local topography (Condit et al. 2000). Trees must therefore have alternative strategies to persist in habitats with a range of topography. Notably, interspecific differences in habitat preferences and tolerances for particular conditions will mean that the density and total basal area of particular species are likely to differ markedly with altitude (Keppel et al. 2010).

1.4 Research aims and objectives

The general aims of this research are to explore the spatial patterns of forests and to investigate forest tree recruitment, mortality and growth in relation to the impacts of cyclone disturbance of intact forests in North Queensland, Australia. Specifically, the aims were to estimate the influence of cyclones on forest structures (i.e stem density and basal area), tree mortality, tree recruitment and tree growth. There are three main hypotheses: first, that both stem density and basal area are lower in areas that had greater frequency of cyclones; second, that cyclones increase tree mortality rates and reduce growth rates; and third, that cyclones have a positive effect on tree recruitment. The reasons for these hypotheses will be explained in the corresponding analysis chapters.

In order to achieve the aims, the objectives of this research are to:

1. Investigate spatial structures of forests, in terms of both the positioning of stems and the distribution of basal area, tree density and tree mortality. (Chapter 3: *Analysis of spatial patterns*)
2. Assess the direct impact of cyclones on the stand level properties of tropical rain forests (Chapter 4: *Stand level effects of cyclone on tropical rain forests*)
3. Investigate factors affecting forest tree mortality and growth mainly based on the individual tree properties (Chapter 5: *Factors affecting mortality and growth rates*)

To accomplish the objectives, the structures of tropical forests will be investigated by comparing spatial patterns before and after cyclone disturbance. In other words, in order to distinguish changes in spatial patterns, post-disturbance growth patterns within the plots will be examined. This involves interpreting differences in the spatial distribution of wood density, identifying the pattern of tree death and spatial relationships between the trees. In order to understand the direct effects of a cyclone, the stand level properties of the forests were analysed using generalised additive models. To assess the influence of individual tree factors and the stand level factor of cyclone on tree mortality and growth rates, the variables were analysed in mixed effects modelling.

1.5 Thesis structure

The first chapter gives an introduction to spatial patterns and the general background. The significance of the research and research aims are also explained. Chapter 2 describes the background of the study area. The CSIRO's survey methods are also described.

Chapter 3 to 5 are the analysis chapters. Chapter 3 analyses spatial patterns of the forest. The analysis focuses on the point patterns of the physical locations of trees, patterns of dead trees and tree density. Interactions between trees are analysed using pair correlation and mark correlation functions. Besides understanding information from the spatial patterns, the chapter focus on changes in patterns following cyclones. Chapter 4 investigates the effects of cyclones on the stand level properties of the forest, which are the total basal area, stem density, stem size inequality, species diversity, tree mortality rates and recruitment rates. Chapter 5 looks at tree death rates and growth rates, which are probably influenced by individual tree factors and cyclones. The individual tree factors here include wood density, family of the trees and crowding effects of trees in the local area. The effects of cyclones on tree mortality are the main focus of this chapter.

Chapter 6 discusses and concludes the overall approaches and results of the research; it explains the research constraints and gives suggestions for future work.

The thesis structure is outlined in Figure 1.2.

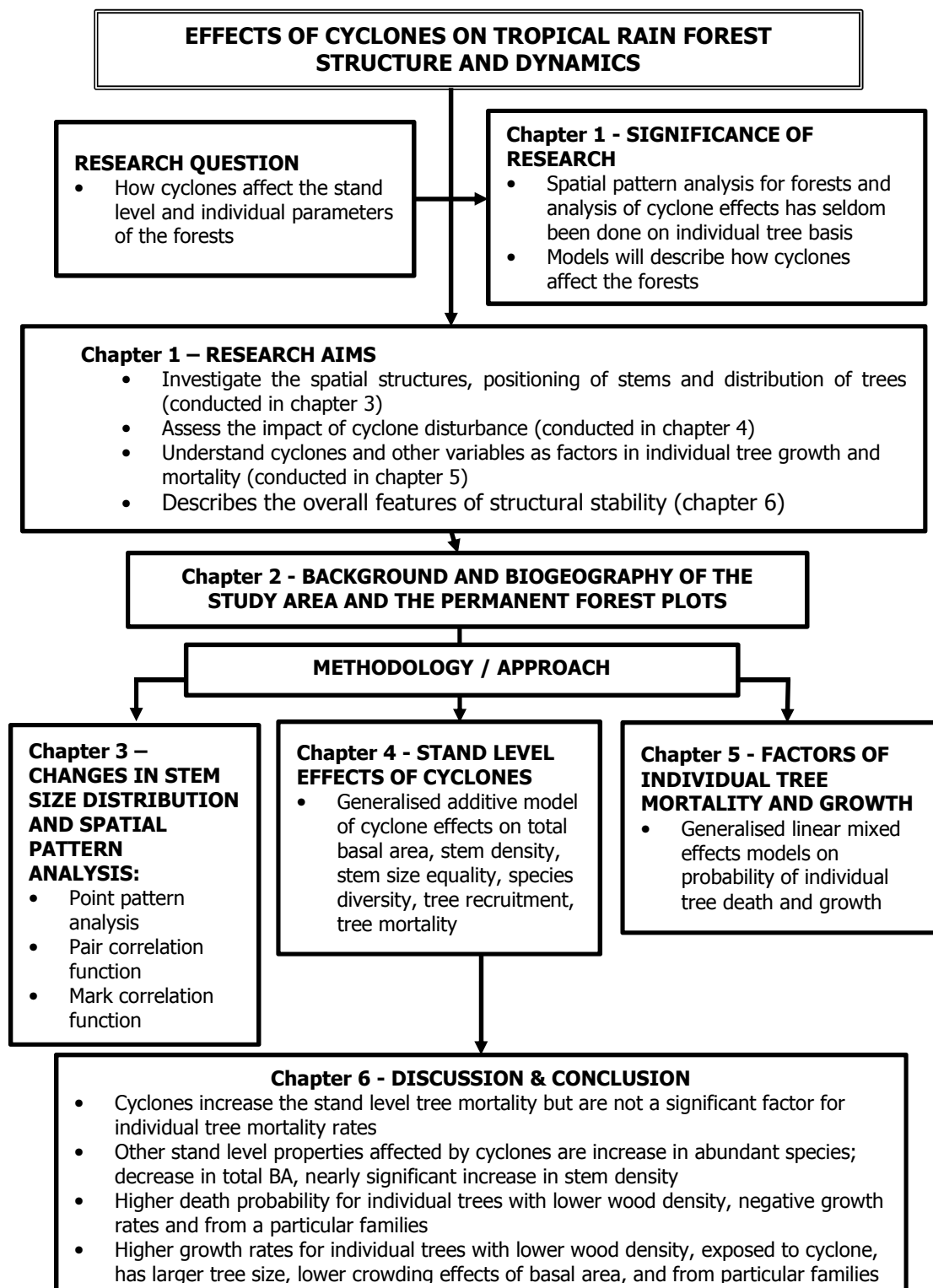


Figure 1.2 The research aims accomplished in Chapters 3 – 5 with brief descriptions on the associated methods and conclusion of the research findings.

2 BACKGROUND OF THE STUDY AREA, DATA SUITABILITY, THE FOREST PLOTS AND DATA PROCESSING

2.1 The study area and the suitability

This study was conducted on the tropical rain forests of North Queensland, Australia. The study area consist of twenty plots situated in the north and far north of Queensland, between $145^{\circ} 04'E$ to $145^{\circ} 50'E$ and $16^{\circ} 08'S$ to $18^{\circ} 30' S$ (Graham 2006) (Figure 2.1). The plots have a rainfall range of 1200 to 3500 mm, represent 11 vegetation types and range from 15 to 1200 m above sea level (Graham 2006, Bradford et al. 2014).

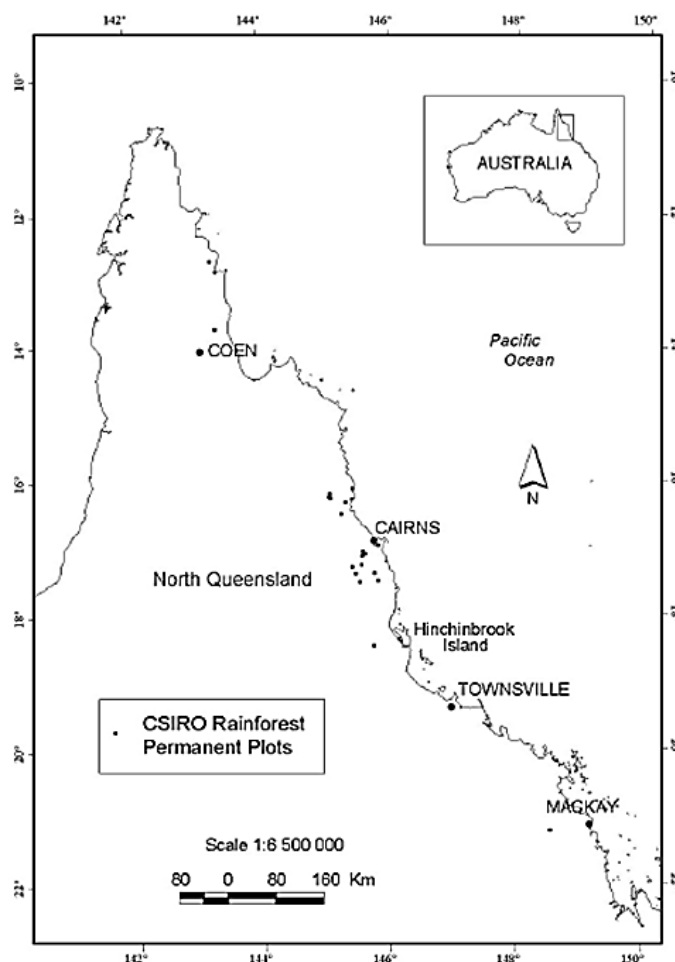


Figure 2.1 The map of the study area (Graham 2006)

As this study aims to investigate the structural stability and impacts of cyclone disturbance on tropical rain forests, it is necessary to use data that have decadal or longer timescales because process affecting forest structure varies over time (Wolf 2005). The data should span several years of observations in order to distinguish structural changes in the forests before and after disturbance. This study used datasets from the 20 permanent forest plots that at least have 30 years of sampling (Table 2.1). The plots are useful in comparative studies of forest dynamics and structural change since they are well-documented and have consistent measurements of dates, growth and mortality events. The project has also published a research report (Graham 2006) with details of physical forest structure, floristic composition, demographic patterns for each species and information on the environment settling such as local climate, geomorphology and soils.

The forest plots provide opportunities to evaluate long term effects of cyclones on the forest structures, tree recruitment, growth and mortality. There were three major or severe cyclones passages since establishment of the plots; in 1986 and two in 2006. Five plots were affected by Cyclone *Winifred* in the year of 1986. In 2006, Cyclone *Larry* occurred on March 20th causing damage to ten plots (Metcalf et al. 2008). In addition, Cyclone *Monica* struck on 19th April 2006 but not much information is available about the impacts of Cyclone *Monica* on the rainforest plots except in a commentary overview (Bellingham 2008). Minor cyclones were also recorded affecting some plots in 1989 (cyclonic winds), 1990 (Cyclone *Joy*), 1999 (Cyclone *Rona*) and 2005. These cyclone events provide opportunities to study the impact of storms on the tropical rain forests in this network of forest plots.

Table 2.1 A summary of enumeration carried out in the twenty CSIRO research plots and observed cyclone events. (Enumeration years marked in grey shades. Abbreviations: EP – Experimental plot, C – Cyclone damage observed. Details for the year of 1971-2005 obtained from Graham (2006). Cyclones observed in 2006 were obtained from Metcalfe et al. (2008). Details on enumeration done in 2006 and 2011 were obtained from currently available datasets.)

Year	Plot																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
	EP2	EP3	EP4	EP9	EP18	EP19	EP29	EP30	EP31	EP32	EP33	EP34	EP35	EP37	EP38	EP40	EP41	EP42	EP43	EP44
1971																				
1972																				
1973																				
1974																				
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1999													C				C			
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2003																				
2004																				
2005																				
2006	C	C	C	C			C		C		C	C			C				C	
2007																				
2008																				
2009																				
2010																				
2011						C														

2.2 The experimental plots

The CSIRO established the long term monitoring sites during 1971 to 1980 which consist of twenty research plots (Table 2.1). The plots were re-measured every two years for the first ten years, and then at three to four year intervals. For each of the CSIRO experimental plots (EP), their characteristics and potentials for cyclone study were summarised in Table 2.2. Some of the characters so far are uncertain whether falls as advantages or constraints category.

Sixteen of the plots have experienced at least once cyclone disturbance since establishment. The other four plots (EP18, EP30, EP39 and EP40) have no records of cyclone damage except for one plot (Plot EP40) where the damage occurred a long time before the plot was established. Cyclone damages in the 16 plots either occurred in enumeration or non-enumeration years. This was considered when assessing the plots analyses. There are 20 records of cyclone damages across sixteen plots, including seven in non-enumeration years.

Each plot being 0.5 ha in size (100 m x 50 m), consist of subplots 'A' to 'P'. All trees within the plots with stems of greater than 10 cm diameter breast height (dbh) were mapped, taxonomically identified and their dbh measured. Individual tree stems were numbered using alphanumeric code that represented both the subplot and number of the stem within that subplot, i.e., in subplot P: P1, P2,... up to potential maximum of P99. Multi-stem tree were also numbered separately with the main stem (example in Photograph 2.1). Epiphytic trees were recorded as well if ≥ 10 cm dbh, but vines were not recorded. There were also data on tree height, but not recorded in every census, hence are not utilised in this research analysis.



Plate 2.1 A multi-stem tree in subplot 'P' of EP35 (Whyanbeel) recorded using additional tree numbers (numbered as P115 from the main tree P15).



Plate 2.2 EP43 (Mount Baldy) immediately after cyclone *Larry* 2006 (Photograph courtesy of CSIRO). Note the fallen dead trunks

Table 2.2 Summary of characteristic and potential of plots for cyclone study

(plot number) Plot name	Plot Characteristics	Other source than Graham (2006)	Advantage	Constraint
(EP2) Downfall Creek	Slightly damaged by Cyclone <i>Larry</i> in 2006	Metcalf et al. (2008)	•	
(EP3) Mount Haig	Slightly damaged by Cyclone <i>Larry</i> in 2006	Metcalf et al. (2008)	•	
(EP4) Little Pine Creek	Cyclone in 1990		•	
	No census made in 7 years (1991-1997)			•
	Forest recovery observed in 1998		•	
	No disturbances other than cyclones		•	
	Irregular canopy or large gap of trees, maybe due to cyclone in 1958 (before plot establishment)		•	
	Among plot with lowest total basal may be caused by repeated cyclones			
(EP9) Robson LA	Moderately damaged by Cyclone <i>Larry</i> in 2006	Metcalf et al. (2008)	•	
(EP18) Mount Lewis	No record of cyclone disturbance			
(EP19) Garrawalt	Damaged by cyclone in 1986 and 2011		•	
	Cyclone damage but non-enumerated years			•
	Disturbances other than cyclones such as canopy dieback caused by of root fungus (observed in 7 years)			•

	Has a highly variable patterns, maybe due to many records of dying trees		•	
(EP29) Mount Fisher	Moderately damaged by Cyclone <i>Larry</i> in 2006	Metcalf et al. (2008)	•	
(EP30) Agapetes Logging Area	No record of cyclone disturbance			
(EP31) Woopan Creek	Severely damaged by Cyclone <i>Larry</i> in 2006	Metcalf et al. (2008)	•	
	Damaged by cyclone in 1986		•	
	No census made in 14 years (1991-2004)			•
	Plot established mainly to study one dominant species that covers 60% of the plot, <i>Backhoosia bancroffi</i>			
(EP32) Little Pine Creek	Slightly damaged by Cyclone <i>Larry</i> in 2006	Metcalf et al. (2008)	•	
	Undisturbed from 1972-2002		•	
	No record of cyclone disturbance		•	
(EP33) Curtain Fig	Moderately damaged by Cyclone <i>Larry</i> in 2006	Metcalf et al. (2008)	•	
(EP34) Russel river	Severely damaged by Cyclone <i>Larry</i> in 2006	Metcalf et al. (2008)	•	
	Damaged by cyclone in 1986		•	
	Large gap and tree fall observed		•	
(EP35) Whyanbeel	Damaged by cyclone in 1986 and 1999		•	
	Forest recovery observed		•	

	Two cyclones disturbance but not in enumerated years (1986 and 1999)			•
(EP37) Eungella	Damaged by cyclone in 1989		•	
	Not enumerated in 1998 (year where tree height measured)			•
	Observed treefalls gaps prior to cyclone		•	
(EP38) The Crater	Moderately damaged by Cyclone <i>Larry</i> in 2006	Metcalfe et al. (2008)	•	
(EP40) Agapetes Scientific Area	No record of cyclone disturbance			
(EP41) Oliver Creek	No record of cyclone disturbance			
	Have evidence of cyclone damage in the vicinity but long before the plot was established			
(EP42) Iron Range	No census made in 6 years (1992-1997)			•
	Other disturbances present but very minor			•
(EP43) Mount Baldy	Experienced erosion as the plot located in a river bed			•
	Cyclone in 1986 and 2006		•	
	Larger tree size compared to other plots		•	
	Moderately damaged by Cyclone <i>Larry</i> in 2006	Metcalfe et al. (2008)	•	
(EP44) Faintail Logging Area	Among most undisturbed plots		•	

2.3 Data Processing

The data set was received partially. The first set of data was received on September 2011 containing plot number, tree number, plant id code, species name, dbh, year measured and status (alive or death) has allowed for basal area calculation. The second set of data were received in early November 2011 containing coordinates for each tree in the plots, with the most recent census date and maximum dbh for each individual trees, had initiates the process for mapping the spatial patterns. Wood density data were received at the end of November 2011, almost completes the data set but still needs extensive amount of data cleaning, validating and finalising. Set of data for this study were updated with the most recent data on May 2014 which available online (Bradford et al. 2014).

Most of the plants species in the CSIRO dataset have full scientific names while some have only herbarium references or are identified to genus. All species names in the dataset were checked thoroughly and individual codes created to simplify further analysis. Nearly all species in the data had an estimate of wood density, though some were absent. Missing data were completed by referring to the Global Wood Density Database (Chave et al. 2009). Some of the species has no available wood density information. In this case, an estimated wood density was arranged by averaging the density of congeneric species (or confamilial where necessary).

The work was carried out mainly using R version 3.1.1 (R Development Core Team 2014). Minor data cleaning and editing were carried out using Microsoft excel and word editors. A unique ID was created for each data rows by combining the plot number, tree number and year measured. Modelling works used statistical packages in R, which will be explained further in the corresponding result chapters.

3 SPATIAL PATTERN ANALYSIS

3.1 Introduction

There are couples ways to infer underlying ecological process from patterns in ecology, where in general involves non-spatial and spatial characteristics of a community. Most commonly, spatial patterns are mainly used as the main approach since could carry information about the processes which operated in the past (Dale 1999, Law et al. 2009). The trees in the forest plots of North Queensland may have some characteristics of spatial patterns based on its natural processes like tree recruitment, growth and mortality, which may be likely modified by disturbances such as cyclone events. Those processes are very common and crucial, thus understanding them from the perspectives of spatial patterns are critically important.

The dataset of the North Queensland tropical rain forest plots could be considered follows a standard model of a long term data (Condit et al. 2014) which provide ideal path for tracing changes in spatial pattern of forests. Several studies have been done on the forest plots of North Queensland Australia, to study forest damages and tree recruitment from cyclone disturbance and changes in stem density of the forests (Metcalf et al. 2008, Murphy et al. 2008, Murphy et al. 2013). However, very little studies points on the spatial patterns of Northern Queensland forest trees. Very little studies analysed the forests in the perspective of spatial point patterns except in several research (examples in Table 3.1). Given the forest of the North Queensland so far has been found with no significant change in stem density over long term data (Murphy et al. 2013) and no studies address on spatial patterning related to cyclone disturbances, this study sought to investigate changes in spatial point pattern prior to the cyclone events on the forest plots.

Table 3.1 Some studies on spatial point pattern of tropical rain forests in North Queensland Australia. The articles obtained from literature search in Mendeley using combinations of 'spatial point pattern', 'tropical forests', 'North Queensland'

Article / Thesis	Spatial pattern	Study
Webber et al. (2010)	Population of a tree species	Exploring possible effects of disturbances to the stand structure and spatial patterning
Pfeifer (2002)	Pioneer tree and non-pioneer tree species	Spatial distribution patterns
Williams et al. (2002)	Small mammals	To relate spatial pattern of vegetation to the mammal assemblage structure

Most importantly, it is crucial to extract information from the spatial patterns because the forests plots hold frequent records of cyclone disturbances. Cyclones are the most destructive type of natural disturbance in tropical rain forests of North Queensland (Bellingham 2008). The cyclones could have profound impacts on the tropical rain forests, but the effects have rarely been examined in the perspective of spatial point pattern. In 2006, cyclone *Larry* significantly damaged many trees in half of the forest plots (Metcalf et al. 2008). In 1986, 25% of the forest plots involved in the cyclone *Winifred* (Graham 2006). The long term data of the forest plots providing opportunity to examine before and after the cyclones.

It is important to extract information on the North Queensland forests from the perspective of spatial patterns based on two reasons. First, little studies are currently available for understanding spatial patterns of the tropical rain forest trees. Second and most importantly, given the forests were surveyed in a long term period, information from the spatial patterns would potentially exposed the impact from the cyclones onto the forests. This chapter mainly involves study of changes in trends of tree size inequality and spatial patterns, also estimations of tree dependence as ways to understand the underlying ecological process of the tropical rain forest trees.

This chapter is to achieve the first objective for this thesis, which is to investigate spatial structures of tropical rain forests and to assess the impact of forest disturbance by cyclones on forest spatial organisation. Furthermore, this chapter will serve some basis to accomplish the second and third objectives of the thesis.

Objectives and hypotheses of study

Generally the analysis of spatial patterns conducted with the data being displayed visually, followed by exploration of patterns and extended with modelling the spatial patterns. This study aims at extract information on the spatial pattern of the tropical rain forest of North Queensland, with emphasis on examining the immediate impact of cyclone disturbance.

More specifically, the objectives of this study are:

- i. to identify changes in patterns of stem sizes, tree density and total basal area in cyclone related years,
- ii. to describe and explore differences of the stand structure and spatial patterns between years by means of maps visualisation, based on tree basal area, tree density and distance between trees,
- iii. to determine interactions between trees using statistical measures.

Hypotheses for this study were made based on factors that may influence spatial patterns of the forests, which are consist of random processes such as tree death; also non-random processes like endogenous and exogenous factors (Murrell 2010). Endogenous factors in focus here are the tree competition and distribution among tree variables, while exogenous factor involved is the cyclone events. The specific hypotheses are:

1. Cyclone event creates higher inequality in basal area size of trees within a plot.
2. Plots with cyclone disturbance would have prominent changes in spatial point patterns

3. Trees in cyclone related plots would cluster immediately after cyclones due to the competition density of new recruiting trees.
4. Distribution of tree size is influenced by the relationship between neighbourhood trees

3.2 Methodology

Diameter at breast height (dbh) and basal areas (BA) of trees were used as baseline data for analysis on spatial structure of the 20 plots. BA was calculated using formulation for the plot, $BA = \sum_{i=1}^n \pi \left(\frac{dbh_i}{2} \right)^2$, where n is the number of stems. Coordinates of each individual tree were plotted as point patterns in R with BA of the trees used as marks. The maps represent the location of each tree with their years and plots.

Four exploratory analyses were performed to test the hypotheses: first, by comparing trends of stem size inequality across years and plots through Gini coefficient; secondly, comparing the forests on cyclone related years based on the tree point patterns of basal area distribution, tree density and distance between trees; the third and fourth involves spatial statistics, which are to understand spatial interaction between location of trees by pair correlation function, and to determine if tree sizes depends on interaction among pair of trees by the final analysis of mark correlation function.

Before conducting the main spatial-statistical approaches, the first attempt to understand the ecological process of the forests also includes non-spatial methods. The aim is to check if there are remarkable trends over the long term dataset. This work involves inspection of trend in total basal area per plot along years and also investigation in inequality of basal areas sizes within a plot via Gini coefficient. This analysis was quite straight forward and simplistic, which may be a reason why this approach seldom been described in literatures. However, these inspection approaches are important as being a preliminary exploratory analysis for this chapter. Conducting this snapshot analysis would help to understand the causes of the spatial point patterns on repeated observations and will yield information (Stoyan and Penttinen 2000). Moreover, Watt (1947) in his expressed paper that:

"It is true that certain recent statistical work is stretching out towards that end, but the application of statistical technique, the formulation of laws and their expression in mathematical terms, will be facilitated if an acceptable qualitative statement of the nature of the relations between the components of the community is first presented."

There could be obvious differences in trends of total BA or irregularity within plot tree sizes that potentially influenced by cyclones. Thus, the total basal areas and Gini coefficient of all enumerated years were inspected thoroughly especially in cyclone affected plots. Information that happens to be available after this work provides as a reference inventory that would be worthy for in depth study of next approaches.

The next approach is the spatial point pattern analysis. The point pattern analysis is a very common method to characterise the spatial patterns and interactions of plant communities (Dale 1999, Law et al. 2009, Picard et al. 2009, Szmyt 2014) because it allows comparative estimates of the spatial distributions of individuals mapped in a given study area. Several main methods for point pattern analysis were reviewed as important by Stoyan and Penttinen (2000) and Perry et al. (2006), but this chapter only conducted methods that appropriate with the nature of the data. The point pattern analysis in this chapter was performed by means of map visualisation of the spatial point patterns and analysis of spatial dependency among trees.

To visualise changes of spatial point patterns following cyclones within a plot, spatial distribution of tree maps were scrutinised on years before and after cyclones, and then compared to an undisturbed year as a control. Twenty maps were produced based on corresponding cyclone events. Map visualisation and comparison were made by investigating changes and differences between nearest surveyed year before and after cyclones (Table

3.2). The total basal area for each plot (Figure 3.1) gives basic pictures of patterns in total basal area that may be related to the cyclone events.

Table 3.2 Comparison of stem density based on cyclone occurrences

Cyclone	Plot	Before cyclone		After cyclone	
		<i>Surveyed year</i>	<i>Total trees</i>	<i>Surveyed year</i>	<i>Total trees</i>
<i>Larry</i> (March 2006)	EP2	2002	537	2006	543
	EP3	2002	491	2006	503
	EP4	2002	448	2006	475
	EP29	2002	474	2006	471
	EP9	2002	465	2006	460
	EP33	2002	277	2006	276
	EP34	2002	279	2006	274
	EP38	2002	355	2006	361
	EP43	2002	364	2006	360
	EP31	2005	229	2013	-incomplete-
<i>Rona</i> (1999)	EP35	1998	465	2002	459
	EP41	1998	337	2002	336
<i>Winifred</i> (1986)	EP34	1984	296	1986	290
	EP43	1984	389	1986	387
	EP31	1984	246	1986	245
	EP19	1985	411	1987	414
	EP35	1985	496	1987	491
<i>Joy</i> (1990) (other cyclonic winds)	EP4	1988	516	1990	516
	EP32	2002	440	2006	449
	EP42	2002	234	2006	250
	EP37	1987	431	1989	439

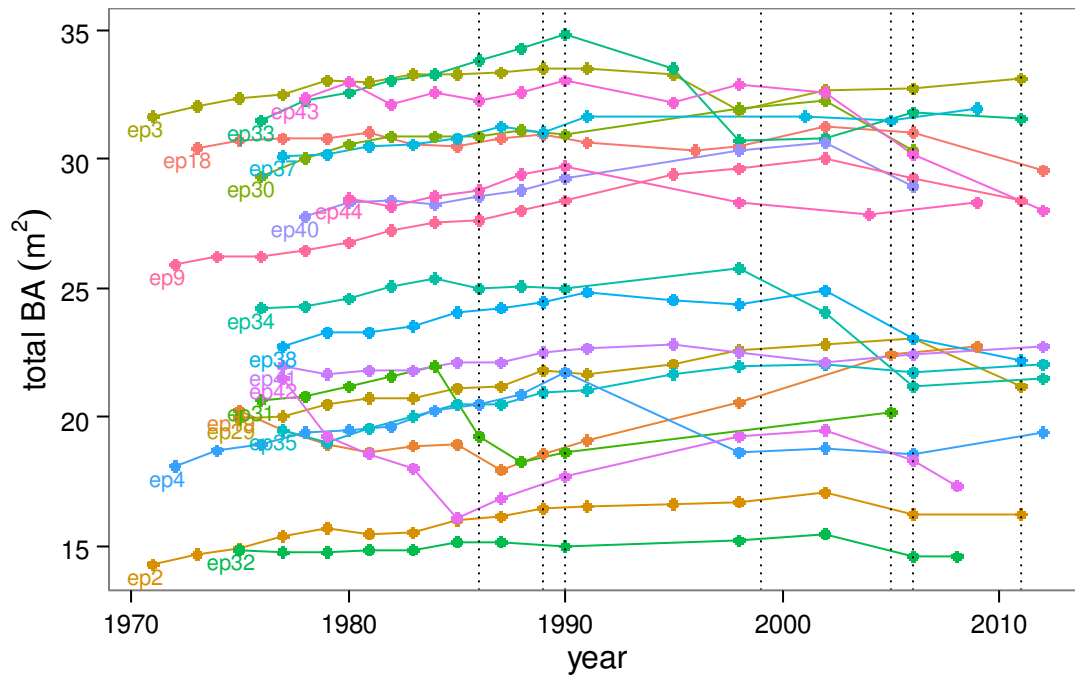


Figure 3.1 The trends of total basal area for each plot. Dotted vertical lines are cyclone event years.

The maps were developed based on the coordinates of trees. Some of the spatial pattern maps specifies with marks of tree characteristics like basal area size, or smoothed as in tree density map or distances among tree map. Commonly, spatial point pattern analysis is to recognise whether the spatial patterns is distributed at random or represents a cluster or regular pattern, but this is not the main concern of this map visualisation approach. The main emphasis with is on detection of spatial patterns or trends which are possibly cyclone-related according to Table 3.2. Focus is more on differentiating spatial point patterns of year before and after cyclone in a way to detect any obvious trends or changes. Interpretation from this approach is expected to assist in extracting additional information from the first non-spatial approaches. This map visualisation is also a practical straightforward approaches for the dataset, as even most non-straightforward *first order* methods are difficult to interpret (Law et al. 2009).

Neighbouring trees would also lead in generating spatial patterns by the tree competitions (Murrell 2010). The pair correlation function is among the most informative statistical measure for analysing spatial point patterns between neighbouring trees (Perry et al. 2006, Law et al. 2009). It delivers true representation of the tree neighbourhood effects by measuring neighbourhood density within relative positions of pairs of trees, which reflects the 'plant's-eye' view (Law et al. 2009). This method is used to assess the consequence of the relationship between tree densities and spatial pattern of trees. Competition are most likely exists between trees within certain distance, therefore indicates as influencing the spatial patterns.

Mark correlation function was also performed to describe the competition structure within relative locations of pair of trees, using tree properties known as mark (Law et al. 2009). The tree points are a fix entity with the marks are randomly located. In this study, tree size was being used as the mark to determine whether distributions of tree sizes are influenced by spatial interaction between trees. The aim is to see whether the tree size is independent from the tree location or not. One advantage in using this method than the non-marked method is the relative location of a tree with respects to the tree neighbours is commonly related to the tree size (Picard et al. 2009).

The analyses all together would help in extracting basic information from intricate spatially correlated plants (Law et al. 2009) in the community like the forest plots, especially from the approaches of pair correlation function and mark correlation function. The analyses that highlights on cyclone related years will possibly give first impression of the effects on tree recruitment, growth and death spatial patterns.

3.2.1 Analysing trends in basal area sizes using Gini coefficient

For comparing trends over years since every plot establishments, Gini coefficient were prepared for each enumerated year and plotted into graphs for visual inspection of trends and patterns. Calculations of Gini were conducted in R *reldist* (Handcock 2013) package. The Gini principally quantified as twice the area between 45 degree line and a Lorenz curve graph (Figure 3.2), which gives output values in the range from 0 to 1. A value close to 1 indicates that individual tree sizes in that particular year of a plot are highly variable, while a value near to 0 suggests similarity in stem sizes. In other words, increasing Gini coefficient means increasing inequality in stem sizes.

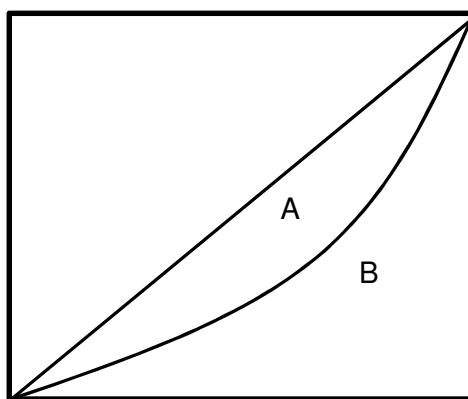


Figure 3.2 Calculating the *Gini coefficient* = $\frac{\text{Area between Lorenz curve and 45 degree line (A)}}{\text{Total area below the line of perfect equality (A+B)}}$

3.2.2 Stand structure and composition of the forests based on point distribution of tree basal area, tree density and distance among trees

For each year within each plot, coordinates of each individual tree were plotted as point patterns in R. Maps were produced according to basal area as marks, using three types of spatial point patterns: BA, tree density or distance among trees. The distribution of the points were plotted into maps using the *spatstat* package in R (Baddeley and Turner 2005). The produced maps provide information of spatial patterns that acquired by visual

comparisons between years of plots for example as in Figure 3.3. Obvious changes in patterns and distribution of the points or the marks may require further investigation. In spite of this, this study has aware that clear differences among all years may not always simple to obtain (Law et al. 2009) because most of the comparison mainly done qualitatively. So, the most practical way is by describing changes in spatial patterns of the tree density, tree basal area, and distance among trees using years before and following cyclone events. The differences of the maps were described qualitatively.

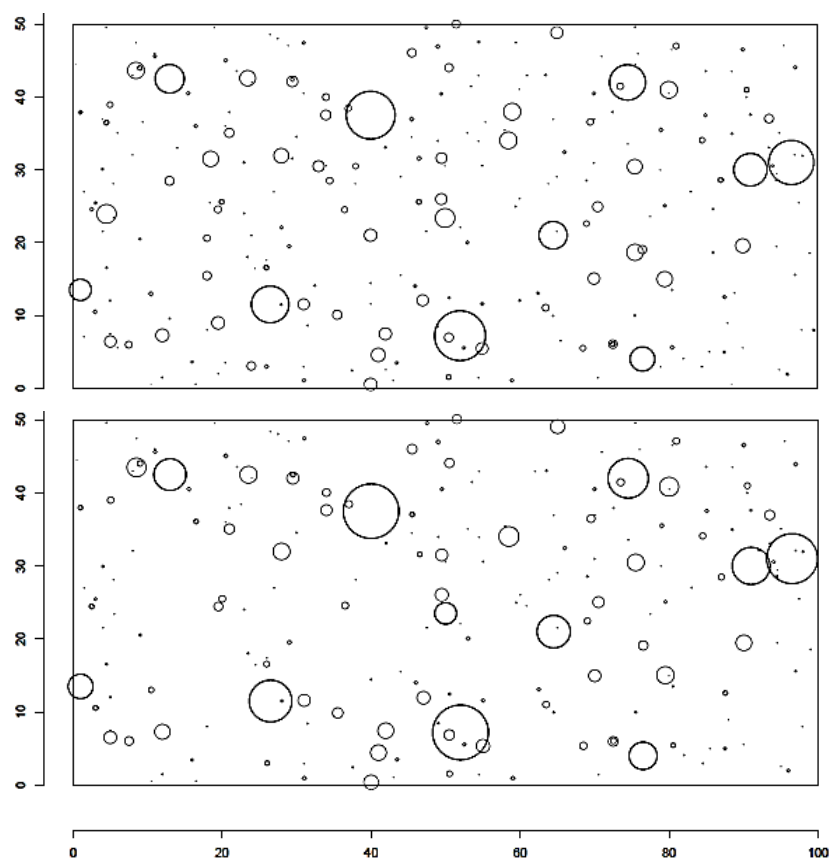


Figure 3.3 An example of map comparisons between two consecutive surveyed year of a plot. Each circle is the location of a tree. The circle radius is proportional to the tree mark (ie. tree basal area)

Tree density and distances among trees were computed by R *spatstat* (Baddeley and Turner 2005) using the tree coordinates and presented in maps. Both maps used basal area as the marks for the points and displays separate information of the tree spatial patterns. The

distance maps (example in Figure 3.4) gives information based on spaces that represent distance among points of trees. While the tree density map (example in Figure 3.5) demonstrates intensity of trees of a surveyed-year within a plot. The tree density and distance map evaluation were carried out is to obtain information on spatial pattern changes between surveys. Intensity of trees was the concern when evaluating the density map, while gap sizes was the main focus in the distance map evaluation. The scale of coloration used on the maps indicates intensity. For density map, dark colour indicates high tree density. For distance maps darker colour represents higher distance of each point in the plot to the nearest and therefore dark patches represent gaps. Sudden appearance of darker colour points suggests new tree gaps in distance map or more trees on density map.

For the entire map comparisons, evaluation codes were created based on the characteristic exists on the map and will be summarised in a table. This study define death intensity as code 3 if number of tree death in the plot is > 10 trees or around 3 % death relative to the average tree density per plot, code 2 if around 6 – 10 tree deaths, code 1 for less than 5 tree deaths. There would be patches of tree crowdedness can be seen from the density map, which categorised as high, moderate and low area of tree density. Location of dead trees were also detected on which crowdedness category within the plot, where $\sqrt{\sqrt{\sqrt{}}}$ means high number of tree death within the patch, $\sqrt{\sqrt{}}$ for moderate number of death and $\sqrt{}$ for small number of death. For the overall intensity of tree crowdedness, comparison made by assigning whether there were increment or reduced in the intensity after cyclone. Code \uparrow if the overall intensity visually increased, code \downarrow for visually decreased and code \sim for lack of change discovered. In term of gap size changes from the distance maps, the codes are: \uparrow if the gap size visually increased, code \downarrow for visually decreased and code \sim for lack of change discovered.

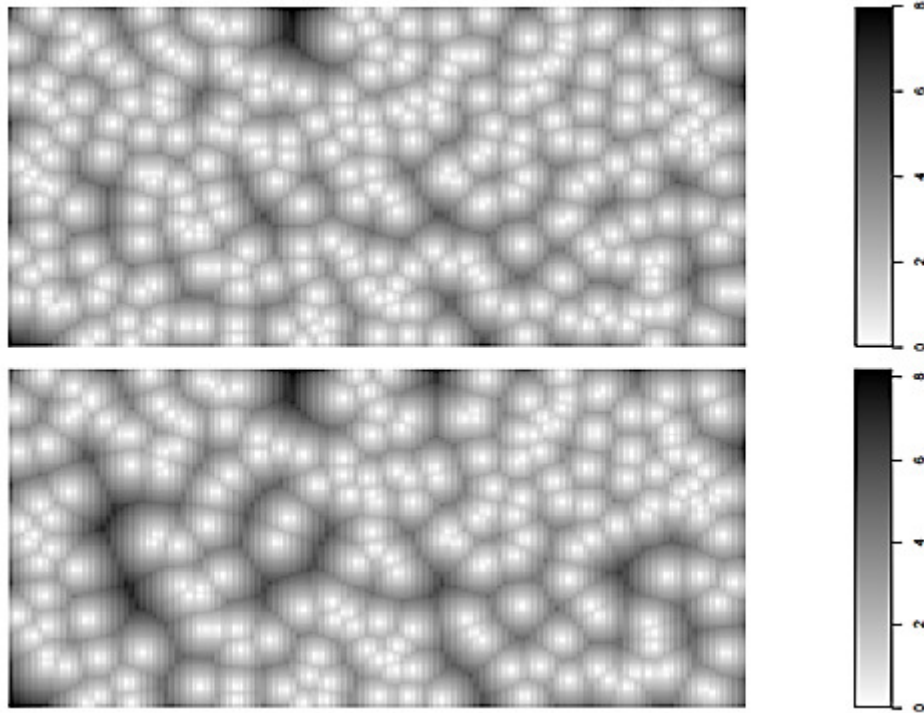


Figure 3.4 An example of tree distance comparison in plot EP34. Year 2002 (above) and 2006 (bottom). Colour intensity is proportional with tree to tree proximity (scale for this particular map is 0 to 5). Light colours are close proximities while darker colours represent low proximity or gaps among trees.

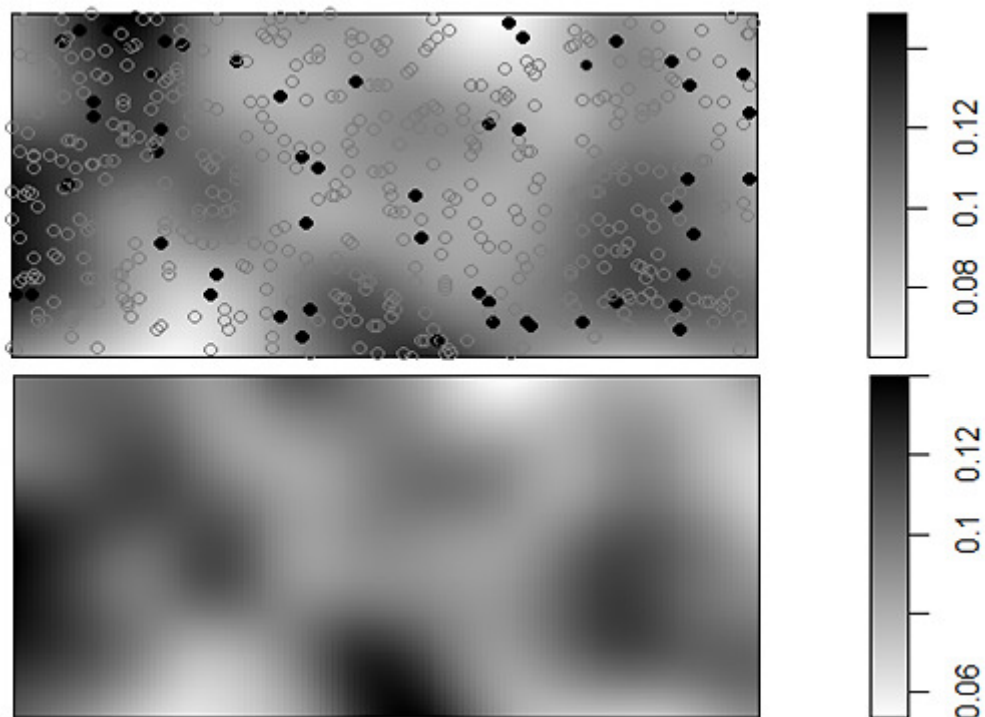


Figure 3.5 An example of tree density map comparison of two surveyed years in plot EP2. Year 2002 (above) and 2006 (bottom). Darker colour represents higher density of stems. Black dots are pattern of tree mortality (stem dbh ≥ 10 cm) in 2006, grey circles are pattern of alive trees.

3.2.3 Spatial point pattern analysis based on pair correlation function

The pair correlation functions for year before and after cyclones were calculated especially for plots that experienced cyclones (Table 3.2). The analysis used 999 iterations of complete spatial randomness for 95% confidence limits of the simulation pairings in the R *spatstat* (Baddeley and Turner 2005) package. An example of output map for this calculation illustrated in Figure 3.6. From the map, a graph line that falls outside the envelope indicates tree densities are dependent on that particular distance, with potential of finding clustered or segregated spatial pattern of trees.

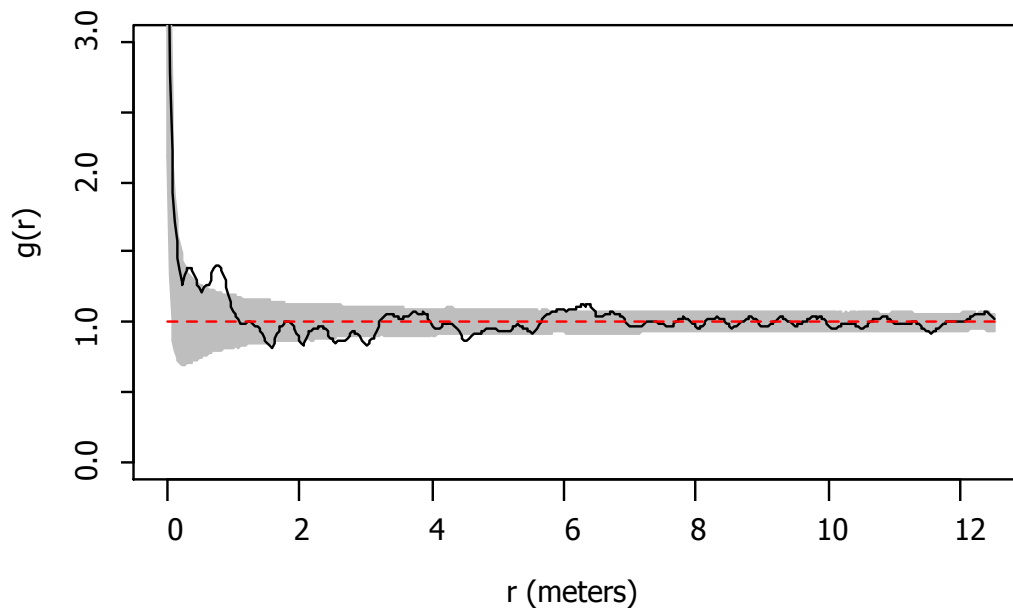


Figure 3.6 An example of pair correlation function output from plot EP2. The black line is the observed value of $g(r)$ for the EP2 2011 data pattern, the dashed line is the theoretical value of $g(r)$ for complete spatial randomness, the grey envelope represent upper and lower pointwise of $g(r)$ from 999 simulations for 95 % confidence limit.

The principal of pair correlation function $g(r)$ has been described in many literatures such as Law et al. (2009) and Picard et al. (2009), which generally in the formula of:

$$\hat{g}(r) = \frac{\hat{K}(r)}{2 \pi r}$$

The $g(r)$ describes cluster, random or segregation of trees at a given radius r , using a standardised density. $\hat{K}(r)$ is the Ripley's K function that calculates average of spatial point patterns within a plot (see Ripley 1977 for details). Tree densities indicated as independent at a given distance if $\hat{g}(r) \sim 1$, which also means random spatial pattern. When $\hat{g}(r) > 1$, means pair of trees are more abundant than the spatial average density of trees at an r distance, and is likely to have clusters of trees. On the contrary, $\hat{g}(r) < 1$ indicates pair of trees are less abundant, where trees are more aggregated. The R software package used this principle of pcf and as illustrated in Figure 3.7.

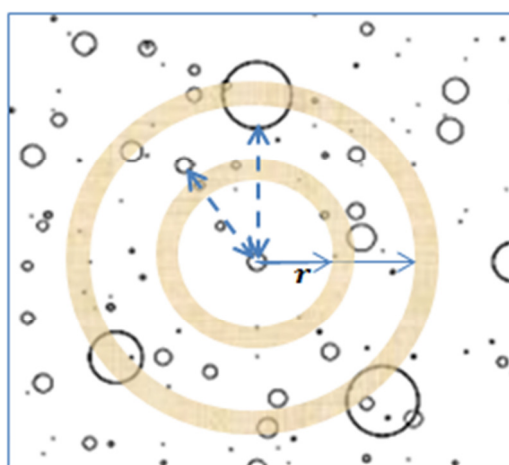


Figure 3.7 Principles to assess pair correlation function $g(r)$. The $g(r)$ will show the relative between locations of pair of trees and spatial tree density within the r distances, with all individuals were assumed equivalent.

3.2.4 Spatial point pattern analysis based on mark correlation function

To assess the consequence of relationship between tree size and spatial pattern of trees, mark correlation function were used. The output for the analysis presented in map for all enumerated years within each plot, which also computed in R *spatstat*. The analysis used 999 iterations of complete spatial randomness to get 95% confidence limits of the simulation pairings.

Patterns of the output graph were used to indicate the spatial pattern processes. An example is shown in Figure 3.8, where if line representing the plot that falls within the simulated envelope suggesting stem size are independent with the tree location. On the contrary, lines that falls outside the 95% confidence envelop suggest tree size is dependent on the tree location at the corresponding distance.

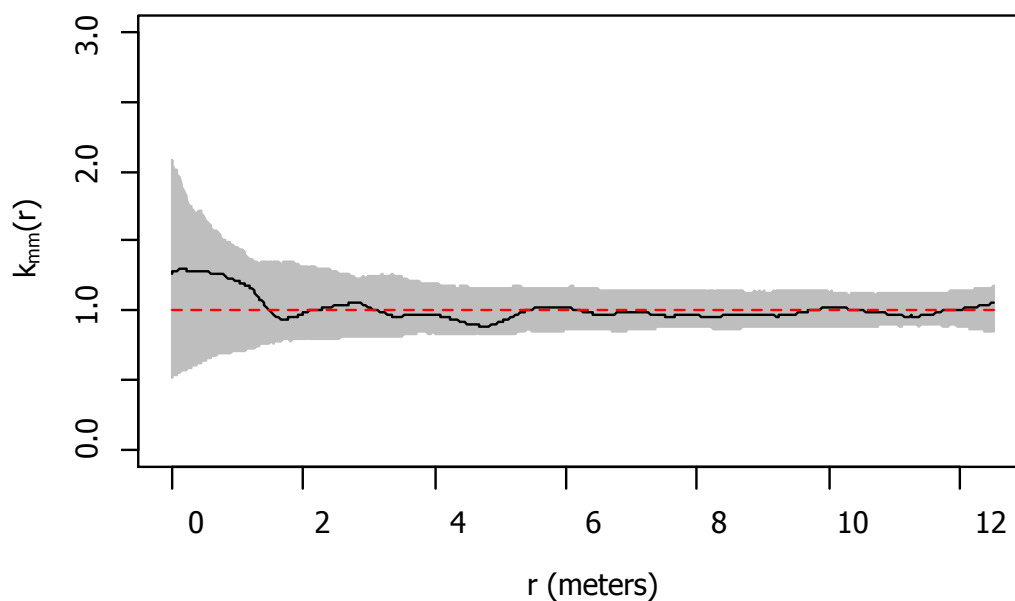


Figure 3.8 Mark correlation function, $k_{mm}(r)$ for plot EP2 in 2011. Black line is the observed value of $k_{mm}(r)$ for EP2 2011 data pattern, the dashed line is the theoretical value of $k_{mm}(r)$ for CSR, the grey envelope represent upper and lower pointwise of $k_{mm}(r)$ from 999 simulations for 95 % confidence limit.

3.3 Results

3.3.1 Inequality of basal area sizes

The Gini coefficients for all plots are shown in Figure 3.9. All plots can be considered as having high inequality in tree size except for one plot (EP2). Highest inequality sizes of tree can be observed in plot EP42 and highest size equality is in plot EP2 (Figure 3.10). There are drastic drops in Gini observed in several plots includes EP42, EP33 and EP38 that indicates equality in sizes were increased, but this is unlikely related to cyclone years. The Gini coefficient for cyclone related years were summarised as in Table 3.3.

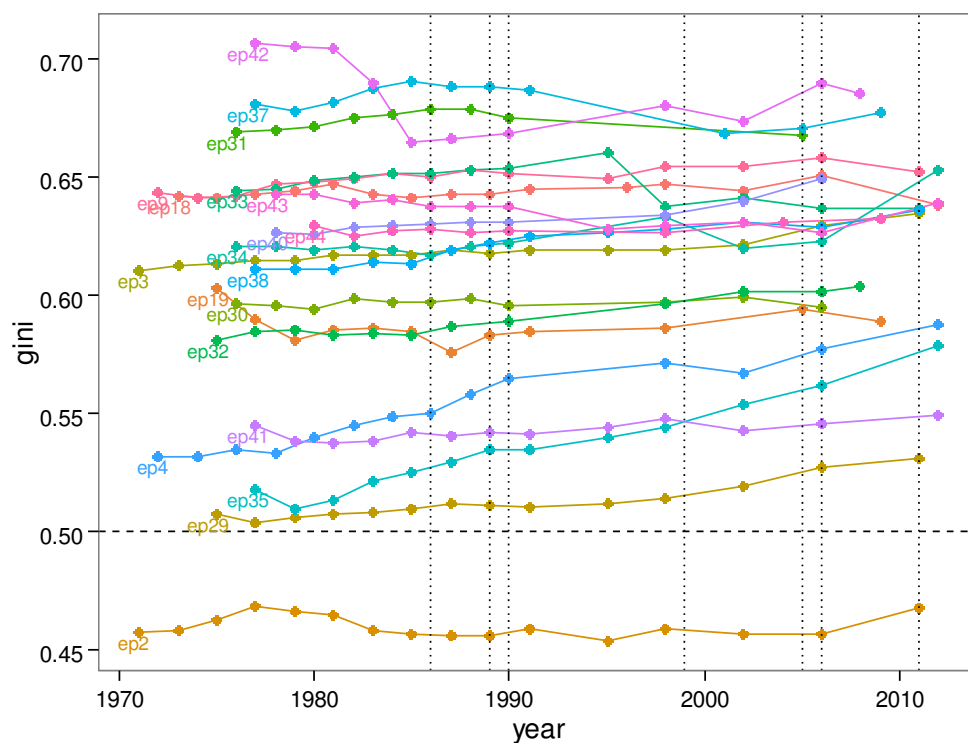


Figure 3.9 Trends of Gini coefficient for all plots. Only one plot closer to 0 (below horizontal dashed line) which indicates more equal sizes tree. Dotted vertical lines represent cyclone event years,

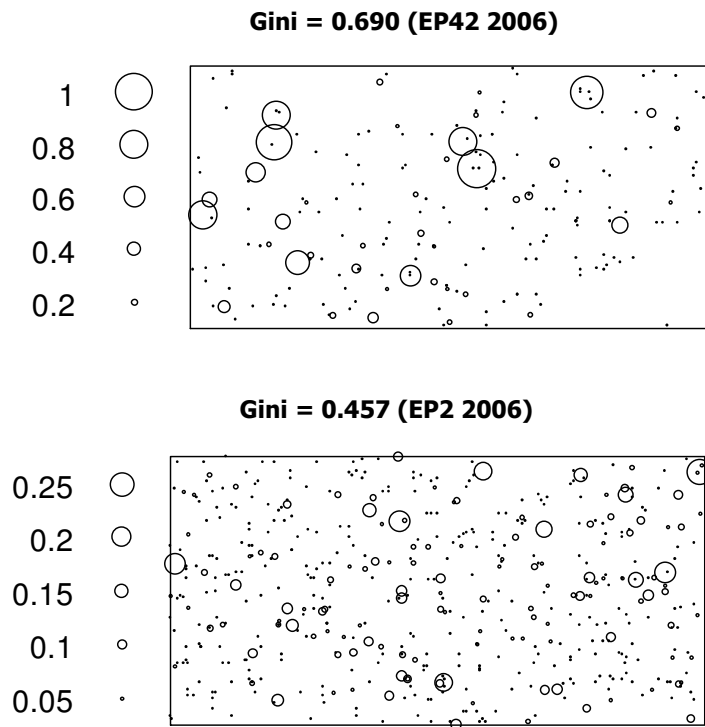


Figure 3.10 The maps showing tree positions and sizes of plot with most unequal basal area sizes (EP42) and plot with highest equality basal area size (plot EP2).

Table 3.3 Summary for Gini coefficient after cyclone in cyclone related plots. Symbol + indicate as increased Gini (higher size inequality), Symbol - is decreased Gini (more equal tree size), ~ is for very slight or no change.

No.	Cyclone	Plot	After cyclone	
			<i>Surveyed</i>	<i>Gini</i>
1.	Larry	EP2	2006	+
2.		EP3	2006	+
3.		EP4	2006	+
4.		EP29	2006	+
5.		EP9	2006	-
6.		EP33	2006	+
7.		EP34	2006	+
8.		EP38	2006	+
9.		EP43	2006	+
10.		EP31	2013	-incomplete-
11.	Rona	EP35	2002	+
12.		EP41	2002	-
13.	Joy	EP4	1990	~
14.	Winifred	EP34	1986	-
15.		EP43	1986	~
16.		EP31	1986	~
17.		EP19	1987	-
18.		EP35	1987	+
19.	(other cyclonic winds)	EP32	2006	+
20.		EP42	2006	+
21.		EP37	1989	-

Plot EP4, EP35, EP29 and EP32 had continuous increases in Gini along almost all surveyed years. This probably indicates as a sign of common forest growth. In other case, Gini increments are also likely increase after a cyclone event as can be seen from the trends along years. Higher inequality or increased of Gini were observed after cyclone *Larry* in 2006 in plot EP2, EP29, EP3, EP32, EP33, EP38, EP4 and EP43. Except for EP9, where this plot has slightly more equal tree sizes with from previous year. Higher Gini also found in EP35 after cyclone *Rona* and other cyclonic winds. It can be inferred that Gini increments is likely to be influenced from cyclones, yet results from map visualisation and statistical measures of the next analyses will strengthen this findings.

3.3.2 Trees spatial pattern

From the map evaluation, basal areas were seen increases across years in all plots. Newly exist points suggest new trees reaching $\text{dbh} \geq 10$ cm and the losses of points means the trees has died. Great number of dead trees was observed in almost all cyclone-affected plots. More specifically, tree deaths were clearly influenced spatial point pattern with death intensity more than 3% relative to the number of tree of the corresponding plot (Table 3.4). The map evaluation also found varying reduction or increment of tree density and size of tree gaps. Table 3.4 summarised the qualitative evaluations of the maps.

Since death intensity or tree deaths were greatly takes place after the cyclones, tree densities were always visually seen lower following cyclones in almost all plots. Density of tree crowdedness was also decreased with the reduced number of trees. Higher tree crowdedness patterns are particularly evident only in EP2 after cyclone *Larry*, probably due to the naturally high number of trees in the plot.

Table 3.4 Summary of map evaluation on plots based on condition following cyclones. The column of total trees before cyclone and total tree increment are used as comparisons. For death intensity, code #3 (high) = more than 3% of tree deaths after cyclone or more than 10 dead trees, #2 (moderate) = 6-10 dead trees, #1 (low) = 5 or less dead trees. Location of dead trees categorised as found within high, moderate and low dense patches of trees, mark with $\sqrt{\sqrt{\sqrt{}}}$ = for high frequency of dead trees found, $\sqrt{\sqrt{}}$ = for moderate frequency, $\sqrt{}$ = for low frequency. For tree density and gap size increment, code \uparrow = increased, \downarrow = decreased, \sim = no change or slightly increased/decreased.

Cyclone	Plot	Year after cyclone	Total trees before cyclone	Number of tree increase/decrease	Death intensity	Death locations (frequency = $\sqrt{}$):			Gap size
						High dense patch	Moderate dense patch	Low dense patch	
<i>Larry</i>	EP2	2006	537	+6	#3	$\sqrt{\sqrt{\sqrt{}}}$	$\sqrt{\sqrt{\sqrt{}}}$	$\sqrt{}$	\uparrow
	EP3	2006	491	+12	#3	$\sqrt{}$	$\sqrt{\sqrt{\sqrt{}}}$	$\sqrt{\sqrt{}}$	\uparrow
	EP4	2006	448	+27	#3	$\sqrt{}$	$\sqrt{\sqrt{\sqrt{}}}$	$\sqrt{}$	\downarrow
	EP29	2006	474	-3	#3	$\sqrt{}$	$\sqrt{\sqrt{\sqrt{}}}$	-	\sim
	EP9	2006	465	-5	#3	$\sqrt{}$	$\sqrt{\sqrt{\sqrt{}}}$	-	\downarrow
	EP33	2006	277	-1	#3	$\sqrt{}$	$\sqrt{\sqrt{\sqrt{}}}$	$\sqrt{}$	\downarrow
	EP34	2006	279	-5	#3	$\sqrt{}$	$\sqrt{\sqrt{\sqrt{}}}$	$\sqrt{\sqrt{\sqrt{}}}$	$\sim\downarrow$
	EP38	2006	355	+6	#3	$\sqrt{}$	$\sqrt{\sqrt{}}$	$\sqrt{\sqrt{\sqrt{}}}$	$\sim\downarrow$
	EP43	2006	364	-4	#3	-	$\sqrt{\sqrt{\sqrt{}}}$	$\sqrt{\sqrt{}}$	\uparrow
	EP31	2006			-	incomplete -			
<i>Rona</i>	EP35	2002	465	-6	#3	$\sqrt{\sqrt{}}$	$\sqrt{\sqrt{\sqrt{}}}$	$\sqrt{}$	\sim
	EP41	2002	337	-1	#2	$\sqrt{\sqrt{}}$	$\sqrt{\sqrt{}}$	-	\sim
<i>Winifred</i>	EP34	1986	296	+6	#3	$\sqrt{\sqrt{}}$	$\sqrt{\sqrt{\sqrt{}}}$	$\sqrt{\sqrt{}}$	$\sim\uparrow$
	EP43	1986	389	-2	#3	$\sqrt{}$	$\sqrt{\sqrt{\sqrt{}}}$	$\sqrt{\sqrt{}}$	$\sim\uparrow$
	EP31	1986	246	-1	#3	$\sqrt{}$	$\sqrt{\sqrt{\sqrt{}}}$	$\sqrt{\sqrt{\sqrt{}}}$	$\sim\uparrow$
	EP19	1987	411	+3	#3	$\sqrt{}$	$\sqrt{\sqrt{\sqrt{}}}$	$\sqrt{}$	\downarrow
	EP35	1987	465	+5	#3	$\sqrt{\sqrt{}}$	$\sqrt{\sqrt{\sqrt{}}}$	$\sqrt{}$	\uparrow
<i>Joy</i> (other cyclonic winds)	EP4	1990	516	\sim	#2	-	$\sqrt{\sqrt{}}$	-	$\sim\downarrow$
	EP32	2006	440	+9	#3	$\sqrt{\sqrt{\sqrt{}}}$	$\sqrt{\sqrt{\sqrt{}}}$	$\sqrt{\sqrt{}}$	\sim
	EP42	2006	234	+16	#3	$\sqrt{\sqrt{\sqrt{}}}$	$\sqrt{\sqrt{}}$	-	\downarrow
	EP37	1989	431	+8	#2	-	$\sqrt{\sqrt{}}$	-	$\sim\downarrow$

Number of tree is generally increased following cyclones in most plots, with decreased in some plots. Four affected plots from cyclone *Larry* had higher number of trees after the cyclone, with the highest new trees was in plot EP4. This is probably due to new recruited trees immediately after the cyclone highly favoured in EP4. The other five affected plots after cyclone *Larry* had slightly lower number of trees, also visually seen as having lower density of stem. From Table 3.4, most affected plots of cyclone *Winifred* had more trees after the cyclone. Several plots had almost the same density of tree in both before and after cyclone, where seen almost visually unchanged. These almost consistent numbers of trees

were plot EP41, EP4, EP43 and EP31. These may indicate that even though the plot had great number of dead trees, the loss most probably replaced by new recruiting trees.

The cyclones also resulted in varying locations of tree death based on level of tree patch crowdedness. The patch that has moderate tree crowdedness is the most frequent location to found tree death in most of the plots. Overall, the map evaluation has revealed dead trees following cyclone events were located in these varying situations:

- i. The most frequent location of dead trees in all cyclone-affected plots was in the moderately crowded patch.
- ii. Relatively low number of dead trees were traced in the high crowding tree patches even the plots has high tree density (except in EP2, Figure 3.11) or even low tree density (except plot EP42 and EP34)
- iii. Relatively moderate number of dead trees were traced in low tree crowding patches especially for plots that have low tree density like plot EP34 (Figure 3.12), EP38 and EP31.

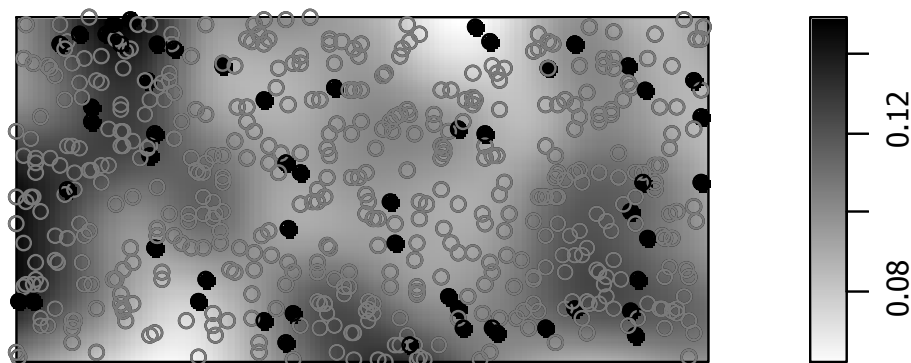


Figure 3.11 Location of dead trees in high total tree density in plot EP2. Dead trees are shown as dark circles. The diameters are not proportional to the tree size. Y-axis shows the scale of the tree density

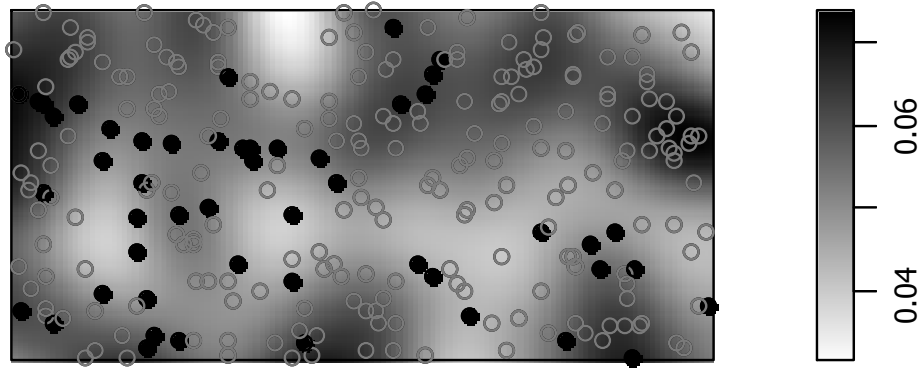


Figure 3.12 Location of dead trees in low total tree density in plot EP34. Dead trees are shown as dark circles. The diameters are not proportional to the tree size. Y-axis shows the scale of the tree density

The density map evaluation found changes in the gap sizes varies greatly, ranging from visually decreased, no change, slightly decreased or increased and prominently increased. Increase in gap sizes is probably be due to damages of trees after cyclones and leaving gaps (Metcalf et al. 2008), while decreasing gaps most probably caused by higher recruitment or density of trees. Although great numbers of tree death visually traced after cyclone *Larry*, increasing gap size pattern was however observed in only three plots out of the nine affected plots. This probably due to tree recruitment that replaces the gap immediately after the cyclone.

3.3.3 Tree interactions

The pair correlation function, $g(r)$ revealed clustered and segregated distribution of trees in some of the plots (Figure 3.13 – 3.16, summarised in Table 3.5). Cyclone *Larry* has been observed to influence spatial patterns at small scale in EP2 and EP33. Cyclone *Winifred* only influences spatial patterns in EP31 also in small scale. There were no significant spatial pattern in affected plots following cyclone *Rona* and *Joy*. All other cyclonic winds also had no significant spatial patterns of the tree pairings except in EP42. However, the spatial point

pattern analysis from mark correlation pattern, $K_{mm}(r)$ has not discover any significant spatial pattern of trees in the plots on year before or after cyclones (Table 3.5).

Table 3.5 Results from pair correlation function $g(r)$ and mark correlation function $K_{mm}(r)$ for all plots that experienced cyclones. Abbreviations:- NS : no significant spatial patterns. +: when $g(r)$ or $K_{mm}(r) > 1$, - : when $g(r)$ or $K_{mm}(r) < 1$.

Cyclone	Plot	Before cyclone			After cyclone			Description
		year	$g(r)$	$K_{mm}(r)$	Year	$g(r)$	$K_{mm}(r)$	
Larry	EP2	2002	NS	NS	2006	+	NS	$g(r) > 1$ at 0.1 - 1 m
	EP3	2002	NS	NS	2006	NS	NS	
	EP4	2002	NS	NS	2006	NS	NS	
	EP29	2002	NS	NS	2006	NS	NS	
	EP9	2002	NS	NS	2006	NS	NS	$g(r) < 1$ at 1.5 - 3 m
	EP33	2002	-	NS	2006	NS	NS	
	EP34	2002	NS	NS	2006	NS	NS	
	EP38	2002	NS	NS	2006	NS	NS	
	EP43	2002	NS	NS	2006	NS	NS	-incomplete data-
	EP31	2005	NS	NS	2013	(nil)	(nil)	
Rona	EP35	1998	NS	NS	2002	NS	NS	$g(r) < 1$ at 0 - 1 m
	EP41	1998	NS	NS	2002	NS	NS	
Winifred	EP34	1984	NS	NS	1986	NS	NS	
	EP43	1984	NS	NS	1986	NS	NS	
	EP31	1984	-	NS	1986	NS	NS	
	EP19	1985	NS	NS	1987	NS	NS	
Joy (other cyclonic winds)	EP35	1985	NS	NS	1987	NS	NS	
	EP4	1988	NS	NS	1990	NS	NS	
	EP32	2002	NS	NS	2006	NS	NS	
	EP42	2002	+	NS	2006	+ & -	NS	
								<ul style="list-style-type: none"> 2002: $g(r) > 1$ at 0 - 1 m, 6 - 7.5 m and 11 - 12 m 2006: $g(r) > 1$ at 0 - 1 m, 6 - 7 m and 11 - 12 m, $g(r) < 1$ at 4 m
	EP37	1987	NS	NS	1989	NS	NS	

After cyclone *Larry* in 2006, the distribution of trees in plot EP2 was clustered at 0.1 - 1 m (Figure 3.13b). This result indicates trees in EP2 are more likely to clump in small scales after cyclones. In plot EP33, the situation was different than EP2. In year 2002 of plot EP33, segregated trees were observed at 1.5 - 3 m (Figure 3.14a & 3.14b) became less segregated after the cyclone (Figure 3.14c & 3.14d). This probably due to relative grows of the segregated trees or loss the trees. Similar patterns with EP33 were observed cyclone *Winifred* affected plot EP31, where before cyclone the cyclone trees were segregated within

small scale of 0.1 – 1 m for the plot (Figure 3.15a), but no significant pattern observed after the cyclone (Figure 3.15b).

Clump of trees in small, middle and large scales within distance of 0.1 – 1 m, 6 – 7 m and 11 – 12 m were observed in plot EP42 that had a cyclonic wind in 2005. However, this phenomenon might not likely influenced by the cyclone since had occurs even before the cyclone year (Figure 3.16a). In spite of that, effect following the cyclone could be seen within 4 m in EP42 where trees are more segregated (Figure 3.16b).

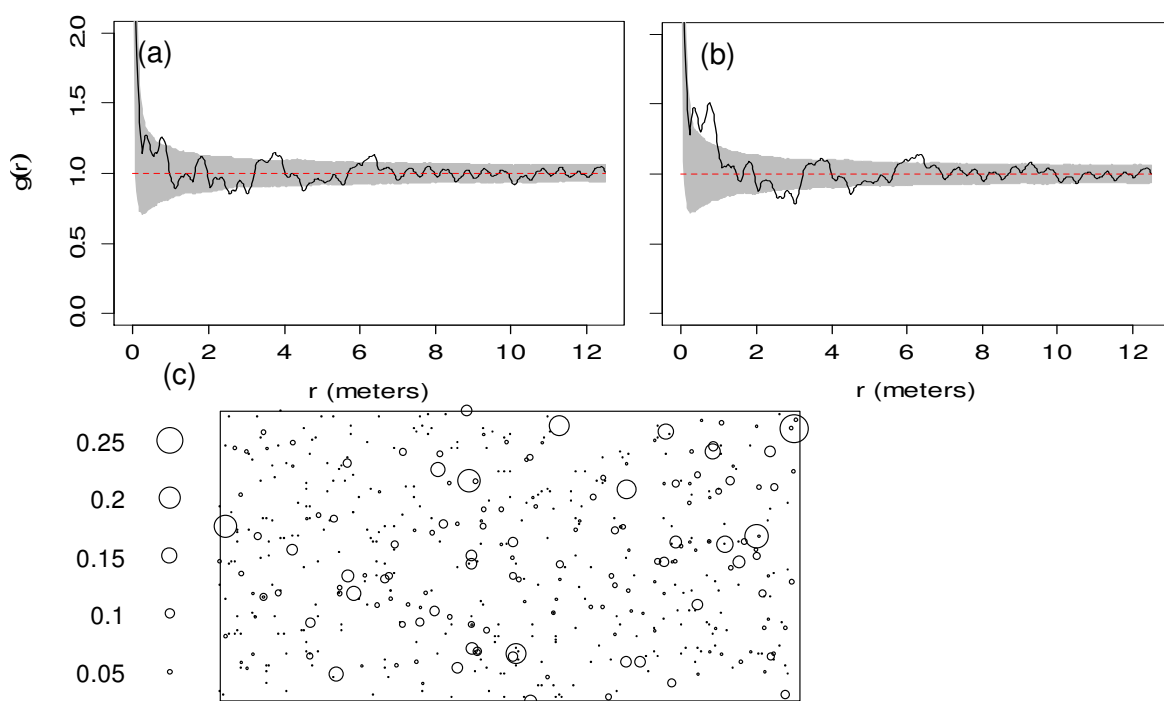


Figure 3.13 Changes in pair correlation of trees can be seen before cyclone *Larry* (a) and after cyclone (b) in plot EP2. Trees were clustered in 2006 after cyclone at 0.1-1 m distance (b), can also be seen form (c)

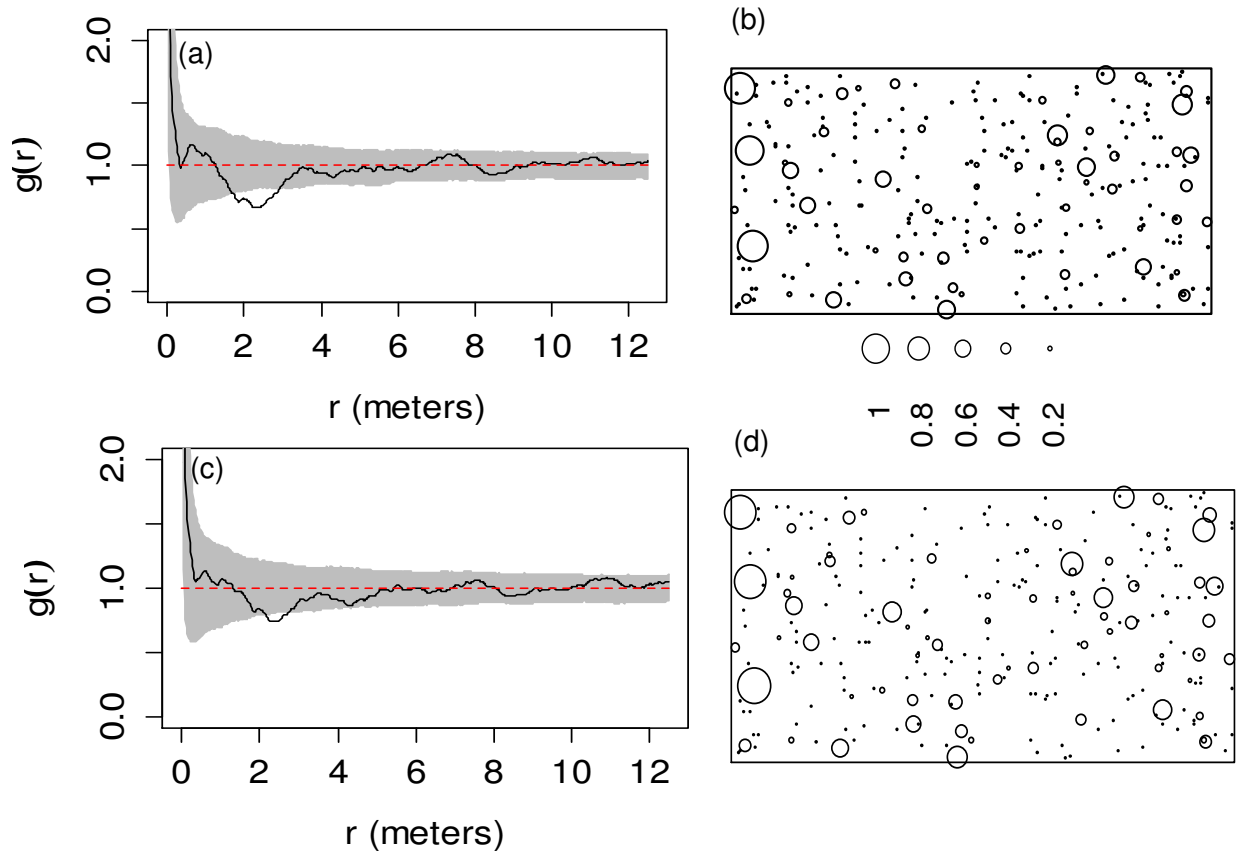


Figure 3.14 Spatial patterns for plot EP33, (a) & (b) are patterns for 2002, while (c) & (d) are patterns for 2006

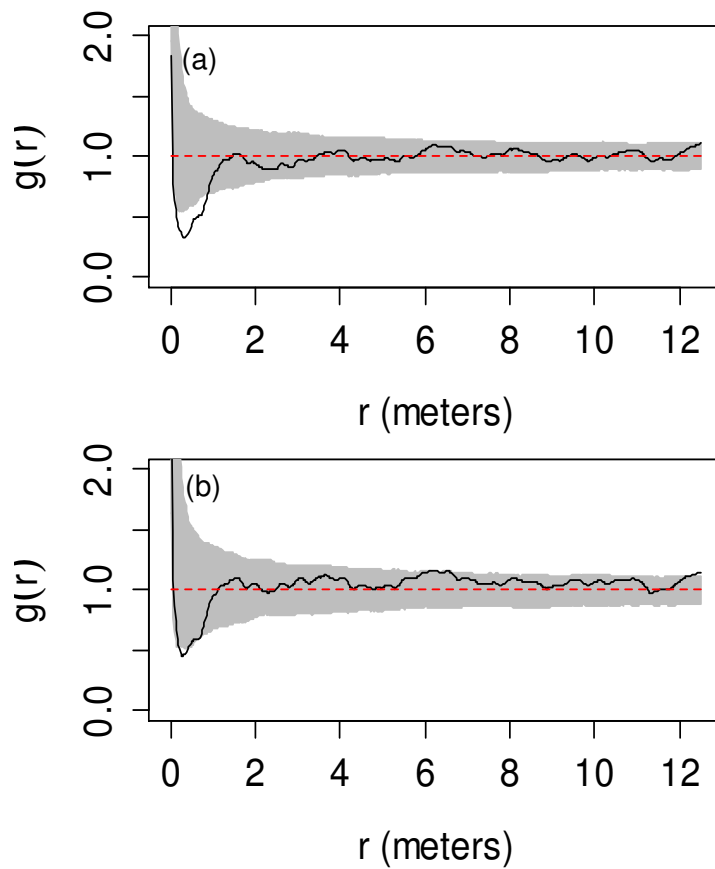


Figure 3.15 Spatial patterns of trees observed from pair correlation function of plot EP31. (a) is in 1984, before the cyclone. While (b) is after the cyclone *Winifred* in 1986

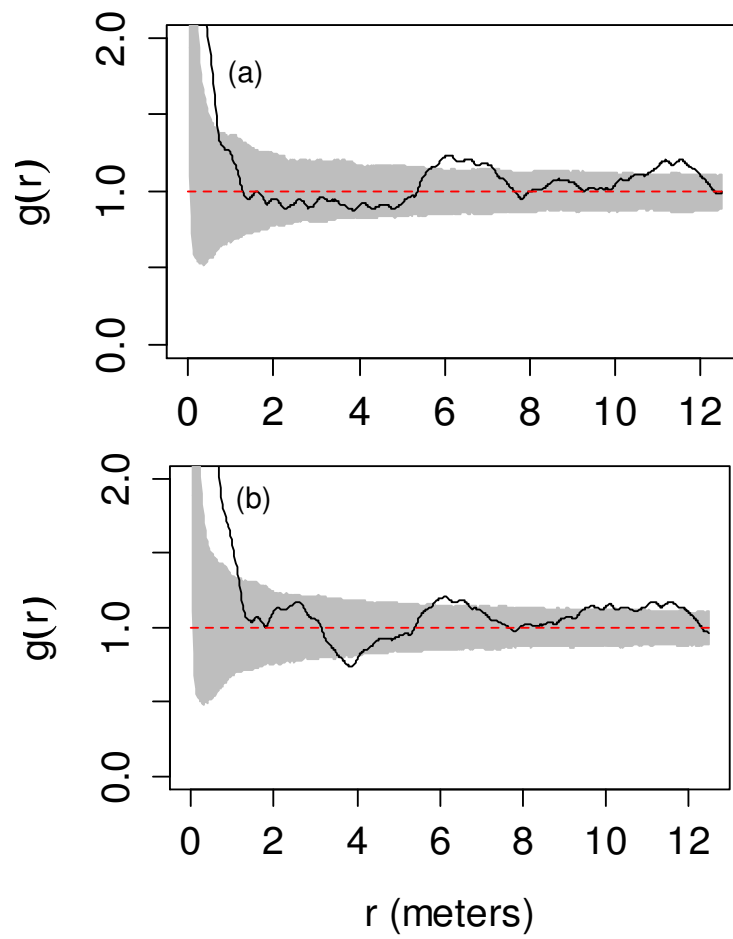


Figure 3.16 Spatial patterns of trees observed from pair correlation function of plot EP42. (a) is during year 2002, while (b) is immediately after cyclone *Larry* in 2006

3.4 Discussion

3.4.1 Spatial patterns per plots after each cyclones

From this study, the variation in spatial patterns following cyclones seems to be influenced from the combination of the plot characteristics. After cyclone *Larry*, it appears that the affected plots responses differently with the cyclone. Especially in plot EP2 and EP33, both has significant spatial pattern of tree pairings but both totally different in term of the features of plots. EP2 has the lowest total BA but highest in tree numbers, has had dropped in total BA after cyclone, increased inequality of tree size and increased tree crowdedness, with clustered trees in small scale. In contrast, plot EP33 that has highest total BA plot but lowest in number of trees, was slightly increased in total BA after cyclone, also increased inequality of tree size, but decreased in tree crowdedness patches with segregated trees in small scale.

Following cyclone *Winifred*, only plot EP31 has shown significant spatial patterns from pair correlation function where trees segregated in small scale, similar to plot EP33. This plot is also has lowest number of trees, moderate total BA and almost no significant change in Gini, which means has consistent distribution of tree size even after cyclone. However, tree size inequality was mostly higher after cyclones in other plots following other cyclones. Cyclone *Larry* brought more inequality of tree size in most of the affected plots.

The intensity of tree death after cyclone *Larry* is generally not consistent with the forest damage level reported by Metcalfe et al. (2008). Whereby this study found the plots has high tree death intensity (more than 3% relative to plot total number of trees) in all ten plots with distinctive changes of tree density after cyclone. However in Metcalfe et al. (2008), level of death are in the range from slight (1 – 10 death) to severe (maximum 36

deaths). Slight damaged levels (less 10 dead trees) observed in EP2, EP3 and EP4 in Metcalfe et al. (2008), but this study has found the three plots experienced high intensity of tree death (at least 10 dead trees or >3%). Although most study claims assessment of forest subsequent changes should be done over a longer time scale, the higher intensity in tree death patterns after cyclone from this study suggests that immediate effects of cyclones from the spatial pattern analysis has provide additional information.

The cyclones also seem to influence tree death based on individual tree locations within levels of tree crowdedness patch. The most frequent location of tree death was within the moderate tree crowdedness. Tree death lower in less dense patches, probably because surrounding trees are conspecific (He and Duncan 2000). Even though this study does not emphasis on the taxonomic identity of the trees, it might be one of the reasons for the lower tree death in less dense patches. Tree death seem lower in high density patches, might be influenced by the common facts that more individuals in an area creates less exposure to cyclone.

Another main issue of the spatial pattern changes is the increment of gap sizes and stem density. The tree density changes created by cyclone *Larry* and *Rona* has distinctive patterns compared with tree density changes created by cyclone *Winifred*, *Joy* and some of the cyclonic winds however the reason remained unsure. Most probably this depends on the time, type or magnitude (Metcalfe et al. 2008) of the cyclone. As observed in plot EP35 that experienced twice cyclone events, tree density was increased after first cyclone but no change or slightly decreased in second cyclone.

Gap size changes were less prominent and almost no significant changes in most plots. But distinctive gap size increment or reduction has been found in several plots with high total number of trees. The gaps were created by death of individual tree or clustered small trees

within the plot. Large gap sizes has imperative role that enhance growth of understorey tree and vitally important for shade intolerant trees. Small gaps from tree mortality may not show any distinctive change after cyclone but still contributes in enhancing the tree growth. Hence, this may be the reason of inconsistent pattern between gap size increment and tree density increment found in all of the forest plots.

From the analysis that investigates tree density dependence, the cyclones have brought significant changes of spatial patterns in only few plots. This changes were traced in plots with low tree density; EP33, EP31 and EP42, and in plot with highest tree density EP2. The analysis has revealed small scale clustered trees in only one plot, which is the plot EP2 that has highest number of tree. Small scale segregated trees was observed in plot with low number of trees like EP31 and EP33. Due to the very small scale patterns found, this study does not perform further analyses consisting separate estimates of $g(r)$ for different BA sizes. But the small scales clustered trees presumably due to the cyclone are more likely has impact on small trees within the plots. This finding overall suggests that spatial patterns of tree density are less likely depends on distance between pair of trees.

Compared to cyclone effects on spatial patterns in other forests, findings from the estimation of spatial pattern are however considered as uncommon. Studies in Paracou French Guyana forest (Picard et al. 2009) and North Carolina forest (Xi et al. 2008) have shown contrast result. The smallest tree range of clustering in the Paracou forest was within 15-60 m which is way further than the clustering distances found in this study. But in terms of plot size, the plots size in this study was quite similar with the minimum plot size in the North Carolina. Small scale tree clustering of less than 5 m also observed in the North Carolina forest, but the range of estimation is up to 50 m. Whereas in this study, the estimation of spatial pattern could only shows up to 12 m. This suggests the whole forest plots in this study are also highly sensitive within very short distance of spatial pattern

estimation. Consequently, very few significant spatial patterns could be traced from this analysis.

For the estimated mark correlation function of tree basal areas, the analysis does not show any significant spatial pattern across all plots and years. This indicates that distribution of tree size is not likely depends on distance between trees. This finding is also very uncommon with many studies that evidence dependency of tree size distribution with neighbouring trees. In other hand, the unavailable significant patterns has raised a speculation where may be due to factor like too large range of data.

3.5 Conclusion

This first result chapter can be summarised as the following diagram (Figure 12):

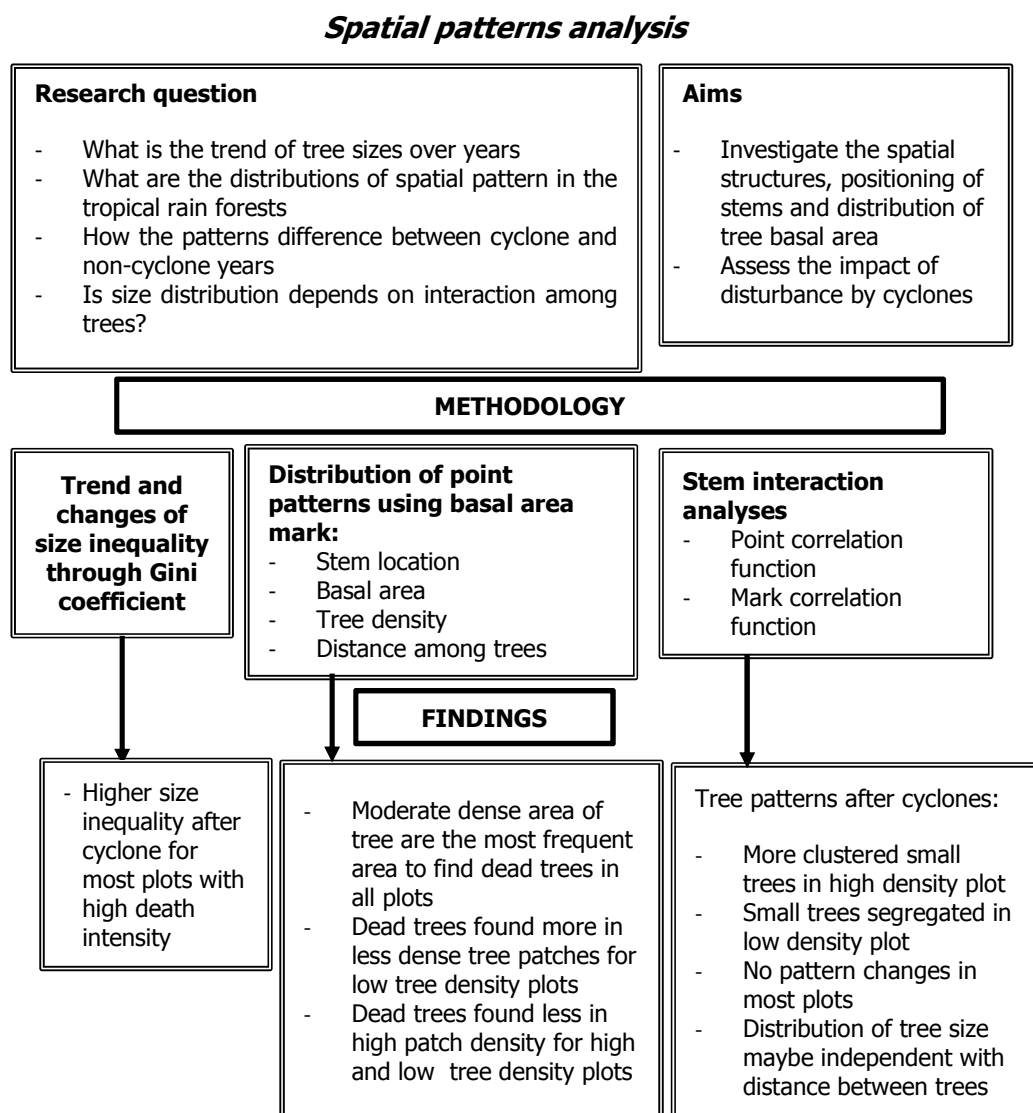


Figure 3.17 The content summary of the Spatial Pattern Analysis chapter

This study, based on forest changes prior to years following cyclone events, demonstrates variable spatial patterns that could be considered as the effect of the cyclones. Absent of significant pattern from analysis of the mark correlation function shall be indicated as independency of tree size from neighbourhood trees, but presumably speculated as having constraint from the nature of the data itself. Nevertheless, all other results from this chapter had at least provides some basic information on the state of the forest plots related to the cyclone events. The noticeable changes from the qualitative observations between patches

of tree density have provide some indication that neighbourhood trees contributes in factors affecting tree deaths. Moreover, the qualitative observation has also revealed new tree points which suggest tree recruitment process. Thus, the qualitative observation suggest that the crowding effects of trees are something necessary to be tested, which will be analysed as crowding effects in later chapters.

Even though the analyses only emphasised changes in spatial pattern from tree density, gap size and tree death after the cyclones, it has also implicitly revealed qualitative information of the tree recruitment. Whereby, the consistent size of tree gaps even in high number of tree death indicates event of tree recruitments took place immediately after the cyclone. Furthermore, results from the visual evaluation of spatial pattern also quite consistent with the trends in the Gini coefficient. High intensity of tree death always resulted in increased inequality of tree sizes which also could be influenced by tree recruitment.

To conclude the qualitative visual inspection, this approach suggests that the spatial patterns of forest trees are likely to form from function of the various factors. Further analysis on the factors is to be expanded from the basic information obtained from this study. Conducting a snapshot analysis for understanding causes of the spatial point patterns especially in repeated observations has yield the basic information, but point process statistic may help to confirm the patterns (Stoyan and Penttinen 2000). Whereby, the basic information will be strengthen by modelling the effects of cyclone and factors affecting tree mortality in the subsequent chapters.

4 STAND-LEVEL EFFECTS OF CYCLONE ON THE TROPICAL RAIN FORESTS

4.1 Introduction

Natural disturbance influences and shapes forest systems by altering their composition, structure and functional processes (Dale et al. 2001). Periodic disturbances such as cyclones are viewed as important elements in forest dynamics because the effects of the cyclones on forest structures are commonly substantial (Lugo 2008, Ghazoul and Sheil 2010, Turton 2012). Cyclones have long been recognised to affect several forests, including on islands and at the edges of continents like the tropical rain forests of Northern Australia (Bellingham 2008). Cyclones have both short and long term effects on the forest structure (De Govenain and Silander 2003, Lugo 2008).

Studies of the short term effects of cyclones focuses on tree damage due to the magnitude and destructive force of cyclones that immediately shows after the event. Tree damage caused by cyclones is normally described by varying levels of destruction of tree communities (e.g., severe/moderate/slight/minor), on individual stems (e.g., no damage/minimal/whole leaf/shredded leaf/twig/branch/snapped/uprooted/smashed) or based on characteristics of the tree (e.g., wood density, species identity and physical location of the tree) (Bellingham 2008, Curran et al. 2008a, Curran et al. 2008b, Metcalfe et al. 2008, Staben and Evans 2008). The probability of a tree damage in forest with frequent cyclones may be relatively lower than in cyclone-prone forests, because the dynamics of the cyclone prone forests has adapted to the frequent cyclone events.

There are varying effects of cyclones on the forests. Within a longer period of time, cyclones are assumed to affect the forests by increasing mortality rates and recruitment rates; but may decrease species diversity, total basal area (BA), stem density (Lewis and Bannar-

Martin 2012). Forest disturbance in general could affect stem size distribution (Coomes and Allen 2007b), therefore the analysis of cyclone effects need to take changes in stem size distribution into account.

Tree damages leads to mortality thus reducing the total BA. Cyclone *Monica* in north Queensland for example significantly decreased the total BA of savannah woodlands (Cook and Goyens 2008). Alternatively no change in total BA was seen after a hurricane in Jamaica (Tanner et al. 2014). This variation in probably because the total BA might or may not be associated the with cyclone disturbance regime (De Gouvenain and Silander 2003). Besides, in several places it has been shown that total basal area recovers quickly after cyclones (Lugo 2008). Total BA of the forests commonly decreases following cyclones also found related to alteration in species diversity (Lugo 2008).

Different species may have different susceptibility to cyclones (Bellingham et al. 1995, Curran et al. 2008a). Certain species can dominate the forest due to better resistance to cyclones. The resistance of a species may relate to their spatial location on the forest landscapes (Ostertag et al. 2005). For example, after a cyclone period in Jamaica montane forests, Bellingham et al. (1995) found trees under closed canopy and on landslides were from resistant species category. Whereas, they found species in gaps were not usually resistant. Plant's functional traits would also a factor influencing species resistance. In north Queensland, species with traits of high wood density were found to have high cyclone resistance and ability to resist damage (Curran et al. 2008a, Curran et al. 2008b). There are also a study explained species resistance in a broader term of species diversity and their relation to forest disturbance levels. Low levels of disturbance will lead to low diversity through the dominance of species that can leave longer, while high levels of disturbance will eliminate species that not possible to sustain in rapid forest colonisation and growth (Catford et al. 2012).

In terms of tree mortality and recruitment rates, both are expected to rise following cyclones as commonly found in any forests facing disturbance, specifically like cyclones. Stem densities of the forests would depend on tree both mortality and recruitment. Since forest disturbances like cyclones were mostly emphasised as leading to tree mortality in many studies, therefore the density of trees are expected to decrease following the disturbance events (De Gouvenain and Silander 2003). Recruitment rates were also expected to rise, considering dead trees leaving forest gaps, exposing lower canopy seedlings to lights which would enhance growth (Coomes and Allen 2007a) and increase the stem size (Coomes and Allen 2007a, Shiels et al. 2010).

Whether cyclones affects forests in the short or long term, both are commonly assessed based on specific attributes of the forests (e.g., location, species) or specific cyclone events (Cook and Goyens 2008, Metcalfe et al. 2008, Murphy et al. 2008). Utilising all occurrences of cyclones has seldom been done. But utilising the available whole stand forest data would closely represent how cyclone affects the forests. This is because it's combine all potential factors that could change forest structure, especially in forests with more than one record of cyclone histories, as in north Queensland. Moreover, a model that utilised whole stand data are usually simple and robust but may involve complexities not possible in other approaches (Vanclay 1994). Therefore, we aimed to determine the direct impact of cyclones across multiple sites, forest types and cyclone events using the whole long term data.

Generalised additive modelling (GAM) is used to fulfil the aims of determining direct effects of cyclones on the forests. The model is fit to the whole stand data. GAM is commonly highlighted as a smoothing model that has flexibility with both linear and nonlinear relationships (Zuur et al. 2009, Robinson et al. 2011). GAM can also maintain variables in their original forms without the need for data transformation (Zuur et al. 2009). The GAM can be extended to a Generalised Additive Mixed Model (GAMM) to connect the response

variables and explanatory variables with random effects of different plot locations and census length of the data. In brief, the GAMM accounts for random effects and heterogeneity attributes to generate a single smooth function.

Given the limited available information on direct impacts of cyclones on forest structures in north Queensland and the capability of the long term forest monitoring data to be analysed using GAMM, we wished to determine to what extent structures change when cyclone occur. The long term data of forest plots used in this study include eighteen records of plots facing major cyclone passages since the first establishment of the forest plots in 1971. The events include Cyclone *Winifred* in 1986, Cyclone *Joy* (1990), Cyclone *Rona* (1999), Cyclone *Larry* and Cyclone *Monica* in 2006, and Cyclone Yasi in 2011. The previous chapter revealed that cyclones are one of the factors driving spatial patterns in the forest plot. With the relatively long time span of observations of the forest plots, it may be possible to further detail the effects of the cyclones on stand-level forest variables: total basal area (BA), tree density, tree size inequality, species diversity, recruitment rates and mortality rates.

The objectives and hypotheses

This chapter aims to determine whether cyclone events have effects on forest structure, and if so, to what extent. The specific objectives were to measure quantitative effects of cyclones on the following variables:

1. Total BA, stem size inequality, stem density
2. Mortality rates and recruitment rates
3. Species diversity (number of species, effective number of common species, effective number of abundant species)

Cyclones were assigned as the main explanatory variable in separate models based on the response variables above. The brief hypotheses were:

1. Lower total BA and more equal stem sizes are likely to occur following cyclone events
2. Cyclones will increase stand level mortality, recruitment rates and stem densities
3. Species diversity will be lower after cyclone events as cyclone-resistant species dominate the forests

4.2 Methodology

4.2.1 Cyclone history

The data from 20 plots in this study have varying records of cyclones and different establishment years (1971 – 1980, Table 4.1). Most of the plots (14 in total) experienced at least one cyclone during the time span of surveys. Six plots have no cyclone records (Mount Lewis (EP18), Agapetes Logging Area (EP30), McIlwraith Range (EP32), Agapetes Scientific Area (EP40), Iron Range (EP42) and Fantail Logging Area (EP44)).

Table 4.1 A summary of the general description of each plot based on Graham (2006), Metcalfe and Bradford (2008) and unofficial records from CSIRO

Plot name (Plot number)	Year plot established	Cyclone	Effect
Downfall Creek (EP2)	1971	Cyclone <i>Larry</i> in 2006	slightly damaged
Mount Haig (EP3)	1971	Cyclone <i>Larry</i> in 2006	slightly damaged
Little Pine Creek (EP4)	1972	Cyclone <i>Joy</i> in 1990 Cyclone <i>Larry</i> in 2006	Cyclone <i>Joy</i> : > 30 large tree uprooted, large canopy gaps, dense understorey Cyclone <i>Larry</i> : slightly damaged
Robson Logging Area (EP9)	1972	Cyclone <i>Larry</i> in 2006	moderately damaged
Mount Lewis (EP18)	1973	No records of cyclone passage	
Garrawalt (EP19)	1975	Cyclone <i>Winifred</i> in 1986 Cyclone <i>Yasi</i> in 2011	Cyclone <i>Winifred</i> : ~10 tree falls Cyclone <i>Yasi</i> : (not reported)
Mount Fisher (EP29)	1975	Cyclone <i>Larry</i> in 2006	moderately damaged
Agapetes Logging Area (EP30)	1976	No records of cyclone passage	
Woopan Creek (EP31)	1976	Cyclone <i>Winifred</i> in 1986 Cyclone <i>Larry</i> in 2006	Cyclone <i>Winifred</i> : 1988 invaded by Stinging Trees Cyclone <i>Larry</i> : severely damaged
McIlwraith Range (EP32)	1975	No records of cyclone passage	
Curtain Fig (EP33)	1976	Cyclone <i>Larry</i> in 2006	moderately damaged

Russell River (EP34)	1976	Cyclone <i>Winifred</i> in 1986 Cyclone <i>Larry</i> in 2006	Cyclone <i>Winifred</i> : some localised gaps Cyclone <i>Larry</i> : severely damaged
Whyanbeel (EP35)	1977	cyclone <i>Winifred</i> in 1986 cyclone <i>Rona</i> 1999	Cyclone <i>Winifred</i> : gap disturbance Cyclone <i>Rona</i> : minor damage
Eungella (EP37)	1977	cyclonic winds in 1989	gap disturbance
The Crater (EP38)	1977	Cyclone <i>Larry</i> in 2006	moderately damaged
Agapetes Scientific Area (EP40)	1978	No records of cyclone passage	
Oliver Creek (EP41)	1977	Cyclone <i>Rona</i> in 1999	Moderate canopy disturbance, most stem remained erect but with some structural injury of branch and foliage loss, most intense structural damage was subplot A and B
Iron Range (EP42)	1977	No records of cyclone passage	
Mount Baldy (EP43)	1978	Cyclone <i>Winifred</i> in 1986 Cyclone <i>Larry</i> in 2006	Cyclone <i>Winifred</i> : minimal damage (few trees lost) Cyclone <i>Larry</i> : moderately damaged
Faintail Logging Area (EP44)	1980	No records of cyclone passage	

Several noticeable characteristics of the plots may be associated with cyclone damage as reported by Graham (2006). For example, topographic wind-funnelling effects (i.e., trees located along valleys or exposed to adjacent cleared land) are likely to produce a higher probability of cyclone damages, as observed in EP2. In EP3, patterns of large tree mortality were concentrated around an ancient landslide (steep sloping sidewalls). Presence of old logs on the ground, small-sized trees and dense shrubs of certain species may indicate the forest plots had experienced cyclone. For example in EP4, the understorey was dense and dominated by *Pandanus* sp. and *Calamus* spp, and trees were relatively abundant with light-responsive species such as *Acacia aulacocarpa*, following cyclone *Joy* in 1990. Forest gaps were immediately dominated by an early coloniser plant species, *Dendrocnide moroides* (Stinging Tree) observed in EP31 after cyclone *Winifred* (1986). These observations are however not regularly recorded and the descriptions are anecdotal. Thus these records were not analysed in this study due to the inconsistent measurement. This study focuses more on the cyclone occurrences shown in Table 4.2. The damage descriptions for the plots are listed

for general background. To understand effects of the cyclones on the forests, only clear measurements recorded from the forest surveys were used: the total basal area ($\text{m}^2 \text{ha}^{-1}$) and the stem density (stems $\geq 10 \text{ cm ha}^{-1}$). Other explicit data were further prepared to study the effects of cyclones.

Table 4.2 A summary of the cyclone records and other main characteristics of the plots based on Graham (2006), Metcalfe and Bradford (2008) and from informal communication with Dan Metcalfe from CSIRO.

Cyclone, year	Affected plots	Cyclone damage characters
Cyclone <i>Winifred</i> , 1986	Garrawalt (EP19)	Around ten tree falls ($\sim 2.5\%$ of trees)
	Woopan Creek (EP31)	Large forest gaps, invaded by Stinging Trees
	Russell River (EP34)	Some localised gaps
	Whyanbeel (EP35)	Gap disturbance noted in 1991
	Mount Baldy (EP43)	Minimal damage (only few stems were lost)
cyclonic winds, 1989	Eungella (EP37)	Gap disturbance
Cyclone <i>Joy</i> , 1990	Little Pine Creek (EP4)	Large canopy gaps (> 30 large trees uprooted)
Cyclone <i>Rona</i> , 1999	Whyanbeel (EP35)	Some damage (tree falls)
	Oliver Creek (EP41)	Moderate damage (7 trees broken), crown damage
Cyclone <i>Larry</i> , 2006	Downfall Creek (EP2)	Slight damage
	Mount Haig (EP3)	
	Little Pine Creek (EP4)	
	Robson Logging Area (EP9)	Moderate damage
	Mount Fisher (EP29)	
	Curtain Fig (EP33)	
	The Crater (EP38)	
	Mount Baldy (EP43)	
	Woopan Creek (EP31)	Severe damage
	Russell River (EP34)	
Cyclone <i>Yasi</i> , 2011	Garrawalt (EP19)	Considerable damage

4.2.2 Data requirements and preparations

Total BA, stem size inequality, stem density, species diversity measurements, mortality rate and recruitment rate were forests variables that could have been affected by cyclone events. These variables were prepared and analysed in separate models as response variables.

Total BA was calculated by summing up every single stem of ≥ 10 cm basal area for each enumerated year for a plot. Tree density was calculated as number of stems ≥ 10 cm dbh present per hectare of each plot per surveyed year. Stand level mortality rate and recruitment rate were in the unit of percentages of dead or recruiting trees (≥ 10 cm dbh) from total available trees in the previous survey. For example, if N_t is the number of trees in year 1983, next census (N_{t+4}) is 1987, thus the percentage is from N_t/N_{t+4} . These stand level percentages were prepared for each surveyed year. To determine stem size inequality, Gini coefficient was used. The Gini is a measure of inequality (see the principle definition in Chapter 3, sub 3.2.1), calculated using the *reldist* package (Handcock 2013) in R. The Gini coefficient provides a quantitative estimate of equality of tree sizes in the range from 0 to 1, which can be calculated as follows:

$$G = | 1 - \sum_{i=0}^n (\sigma Y_{i-1} + \sigma Y_i)(\sigma X_i - \sigma X_{i-1}) |$$

Where n = number of individuals, Y_i = observed proportional area of each individuals, X_i = expected proportional area of each individuals if area were distributed equally, σY = accumulated proportions of Y values and σX = accumulated proportions of X values. A Gini close to 1 indicates individual tree sizes in a particular year of a plot are highly unequal, while a value near to 0 suggests complete equality in stem sizes.

For analysing effects of cyclones on species diversity, species diversity was quantified using Hill's numbers (Hill 1973). These incorporated actual number of species: *Chao* (0D), the Shannon index (1D) and the Simpson index (2D); which are considered the most consistent measurements for species diversity (Tuomisto 2010, Chao et al. 2012). Hill's numbers can be described in the order of q in qD , where parameter q weights towards rare or abundance species (Hill 1973, Jost 2006, Tuomisto 2010). In general, the indexes represent the number of equally common species and known as the 'effective number of species'. Large values of q weight indices towards the effective number of the most abundant species, while small

values of q weight towards the effective number of rare species. Diversity can be quantified for any dataset where units of individuals have been classified into species. The principle used in quantifying the diversity of the species is what proportion of the observed units belongs to a type of mean abundance. The unit of the observed diversity will change accordingly, e.g. effective number of the types of interest is quantified by diversity equals the inverse of the mean abundance (Tuomisto 2010). If all species are equally abundant, then there are as many effective species as actual species. Otherwise, there are fewer effective than actual species.

At $q = 0$ or 0D , diversity represents the species richness. The Shannon index (1D) is the effective of common species, while species Simpson index (2D) is the effective number of abundant species which describes dominance. The species diversity measurements (i.e., 0D , 1D and 2D) for each year within plots were prepared using the *vegan* package (Oksanen et al. 2013) in R. These diversity measurements were assigned as the explanatory variables. Effects of cyclones will be analysed by any significant increase or decrease of the effective number of the indexes. If the indexes significantly changed whether higher or lower following cyclones, this means cyclones affecting the species to become relatively more or less diverse. For example if the tree community within a plot has an index diversity of 20.8 and 21.3 effective species before cyclones and after cyclone, the cyclones can be say has increase 1.02 times the diversity in the community. The value of the index is not necessarily important because the index itself is not a diversity, but the increases or drop in the diversity percentages is important.

4.2.3 Modelling effects of cyclones

To identify how cyclones affect the forest variables, analyses were done using the generalised additive mixed modelling (GAMM). This modelling approach was used because it

allows arbitrary specification for each response variable included in the model and accounts for mixed effects from multiple surveyed years on the same plots and also between plots. The GAMM was fitted into regression splines to model the effects of cyclone for any year of forest surveys, where the regression spline was used to reflect the year pattern. GAMMs in this study were used to test for effects of cyclones on response variables of (i) total BA, (ii) tree size inequality (measured as Gini coefficient), (iii) stem densities, (iv) overall mortality rates, (v) overall recruitment rates and (vi) species diversity. Models were all assigned as

$$Y = f(x_t) + \beta_1 \times \text{cyclones} + \gamma_p + \varepsilon$$

Where each response variable of Y was modelled as the function of year surveyed ($t = 1971, \dots, 2011$) that was accounted using smoother function $f(x_t)$; binary fixed effects (either yes or no) of cyclones; and the variation among forest plots ($p = \text{plot } 1, \dots, \text{plot } 20$) accounted as random effects γ_p . The covariates were used since the starting model and subsequent processes of the analyses (Figure 4.1). The model therefore effectively identifies the effect of cyclones on the tested response variable.

The analysis processes followed general modelling protocols as in Zuur et al. (2009) and Zuur et al. (2010). No formal way to estimate model fit for GAMM, but several intermediate models may be required during the modelling process (Zuur et al. 2009). The GAMMs in this study involved intermediates such as linear models (LM) to capture background of the analysis, generalised least square (GLS) to fit the extended linear model and linear mixed effects model (LME) to fit in the random argument for GAMM (Figure 4.1). The LMs were processed using the R package *lme4* (Bates et al. 2014), GLS and LME in R package *nlme* (Pinheiro et al. 2014), while the GAMMs used R package *mgcv* (Wood 2011). The intermediate models before GAMMs were also needed for other purposes. For example, to account for the heterogeneity features of the data, on optimal variance structure determined during Restricted Maximum Likelihood (REML) estimation under the GLS modelling process. Akaike Information Criterion (AIC) values were used in each modelling step to find an

optimal model, where lowest AIC indicates a relatively better fitting model. For example, the AIC supported that the GAMM in this study accounted for more deviance than the normal GAM, therefore inclusion of random effects was an improvement.

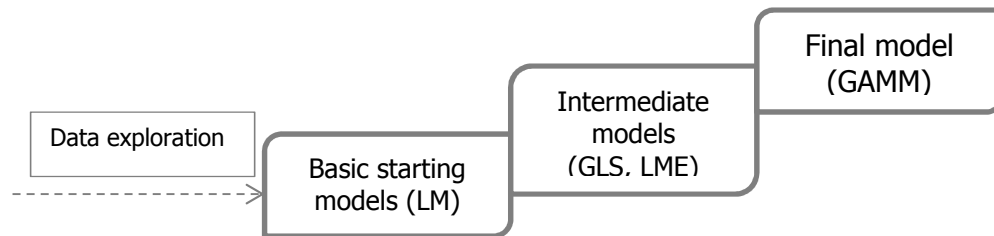


Figure 4.1 Mixed modelling steps as suggested by Zuur et al. (2009)

4.3 Results

Cyclones significantly increased the effective number of abundant species and mortality rates of the forests ($p < 0.001$). Effects on the tree density were close to significance ($p < 0.1$). In contrast, cyclones reduced the total BA concurrent with a significant increase in mortality rates. There were no cyclone effects on tree size inequality, effective number of common species, number of species or recruitment rate. Table 4.3 summarises all the results.

Table 4.3 Summary of the results of all nine variables in this study, analysed in separate GAMs

Response variables	Cyclone effects		
	Positive	Negative	p-value
Total BA ($\text{m}^2 \text{ ha}^{-1}$)	-	0.703 ± 0.08	< 0.001
Tree density (stems $\geq 10 \text{ cm ha}^{-1}$)	4.65 ± 2.5	-	0.065
Tree size inequality (Gini coefficient)	-	-	0.673
Effective number of common species, ¹ D per	-	-	0.245
Effective number of abundant species, ² D per	0.121 ± 0.04	-	0.03
Species richness (Chao) per plot	-	-	0.263
Recruitment rate (% year ⁻¹)	-	-	0.602
Mortality rate (% year ⁻¹)	1.39 ± 0.11	-	< 0.001

4.3.1 Effects of cyclones on total basal area

Generally, the forest plots had varying patterns of total BA along enumerated years (Figure 4.2). Over the whole dataset, the majority of plots initially had increasing trends in total BA but this slowed during late 90s, and started to decrease after 2000s (Figure 4.3). As seen in Figure 4.2, the plots faced Cyclone *Winifred* in 1986, cyclonic winds in 1989 and Cyclone *Joy* in 1990, Cyclone *Rona* in 1999, Cyclone *Larry* in 2006 and Cyclone *Yasi* in 2011. The number of plots affected by cyclones before 2000 were relatively lower than after 2000, which may be one factor in the decreasing trends of total BA in most plots (Figure 4.2). The GAM found

that $0.703 \pm 0.08 \text{ m}^2 \text{ ha}^{-1}$ of total BA in the forests were lost after each passage of cyclone per plots ($t = -4.304, p < 0.001$).

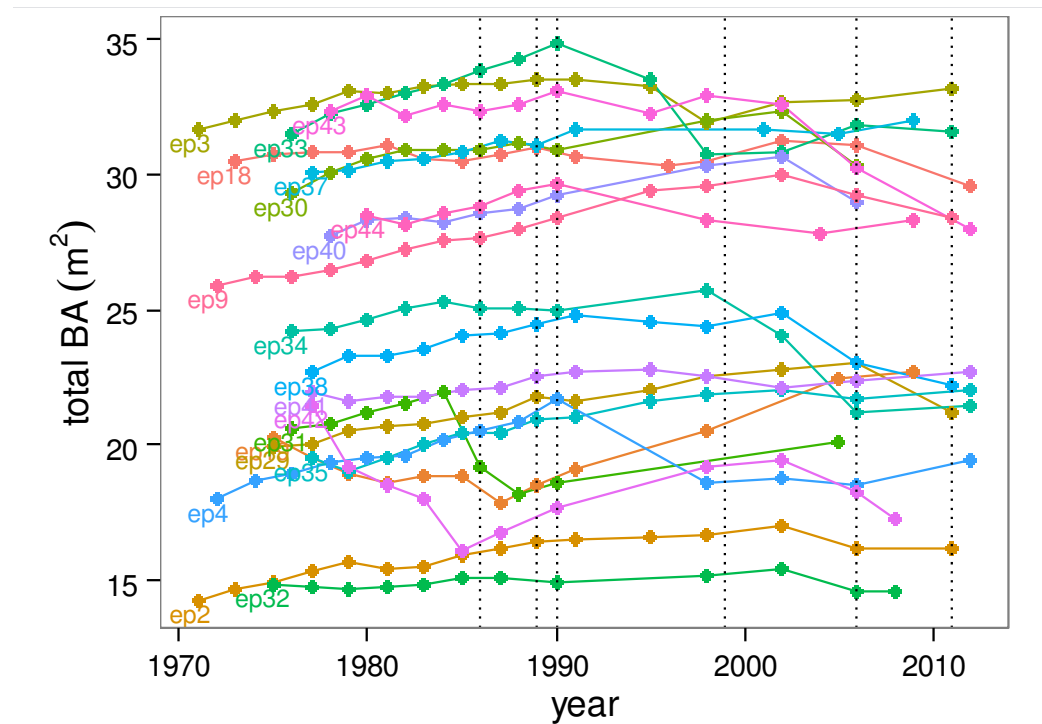


Figure 4.2 Trends of total basal area for each plot. Dotted vertical lines are cyclone event years

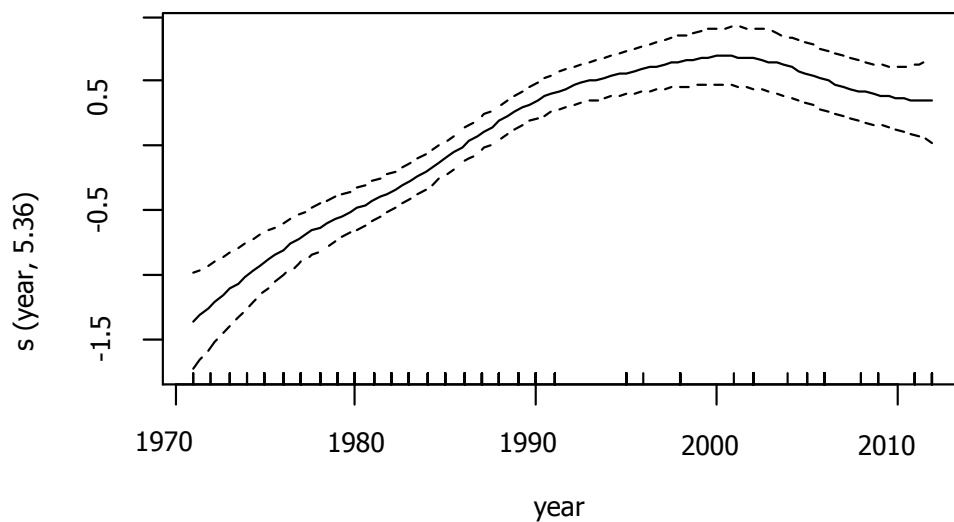


Figure 4.3 Smooth spline fit for total BA. The y-axis is relative to time-averaged mean for the total BA under estimated degrees of freedom 5.36. The dashed-bars are 95% pointwise confidence intervals.

4.3.2 Effects of cyclones on stem densities

Stem density decreased with time in most of the plots (Figure 4.4), demonstrated in the GAM plot (Figure 4.5). Cyclones were found to have a near-significant positive effect on stem density ($t = 1.85$, $p = 0.065$), where the GAM estimated around 4.65 ± 2.5 trees ha^{-1} recruit in the forest plots after each cyclone.

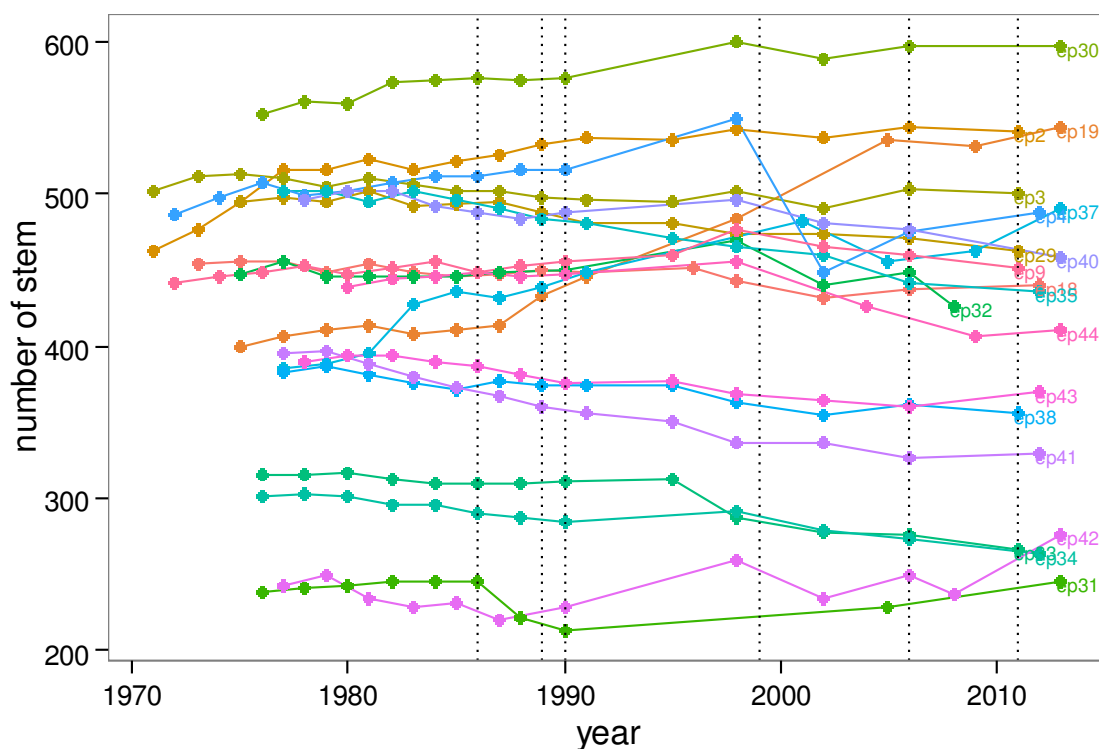


Figure 4.4 Stem density in each plot. Dotted vertical lines are cyclone event years

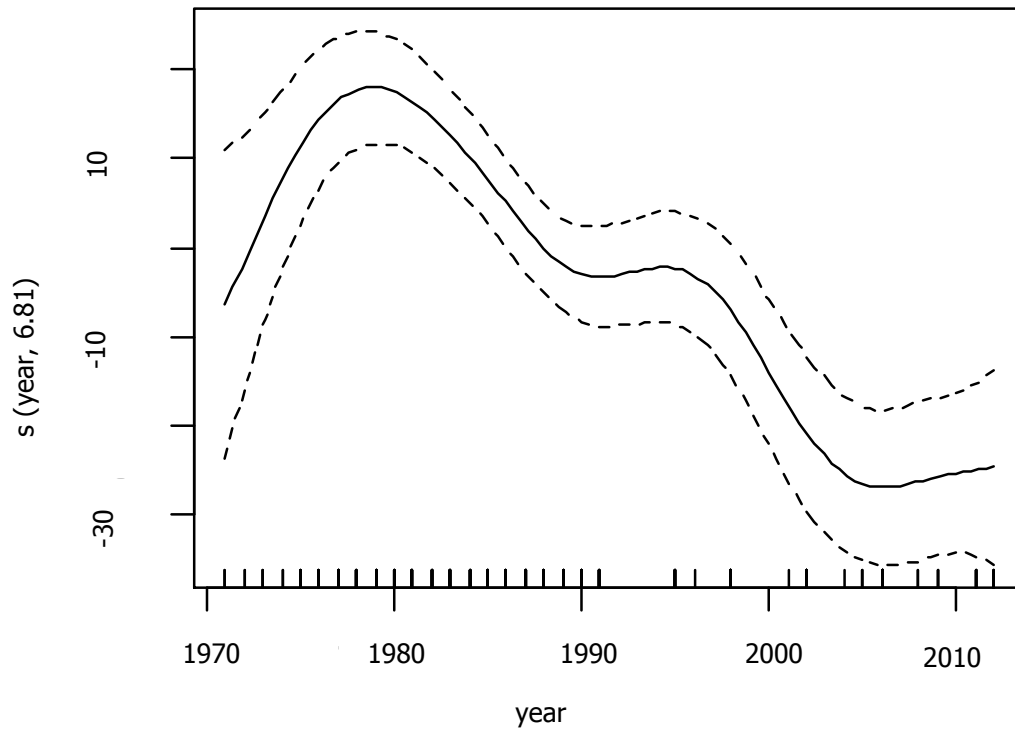


Figure 4.5 Smooth spline fit to time series of stem densities since establishment of all plots with value of y-axis relative to time-averaged mean, under degree of freedom 6.8.

4.3.3 Effects of cyclones on tree size equality (Gini coefficient)

From the GAM, there is an increasing trend in Gini coefficient over time (Figure 4.6) which mean tree sizes became more unequal on average across the plots. As can be seen from Figure 4.7, changes in Gini over years were relatively small for most of the plots. There was no significant effect of cyclones on the Gini coefficients overall ($p = 0.673$).

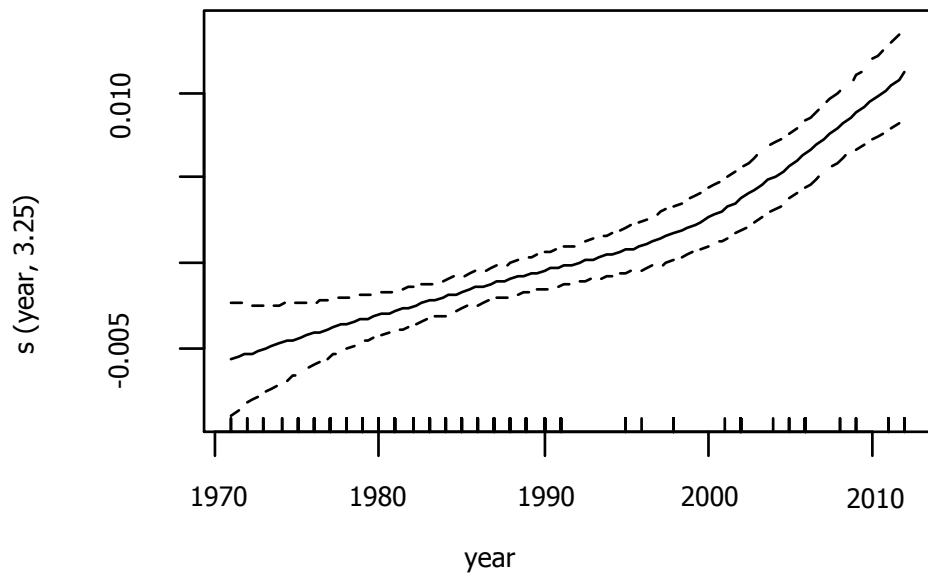


Figure 4.6 GAM plot shows smooth spline fit to time series of Gini since establishment of all plots with value of y-axis relative to time-averaged mean, under degree of freedom 3.25.

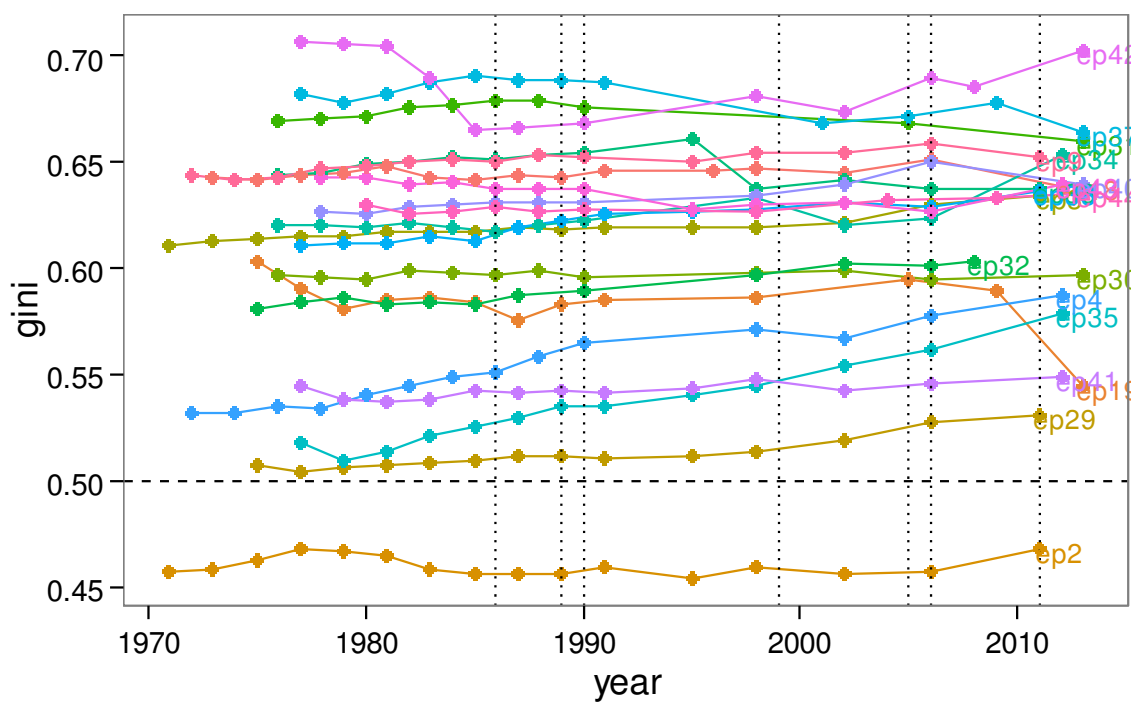


Figure 4.7 Gini coefficient in each plot. Dotted vertical lines are cyclone event years

4.3.4 Effects of cyclones on species richness (Chao)

Most of the forest plots had slight changes in species richness (*Chao*, 0D) along the enumerated years (Figure 4.8). Some plots were has fluctuated patterns. The GAM shows that those patterns indicates species richness were not influenced by cyclones ($p = 0.263$).

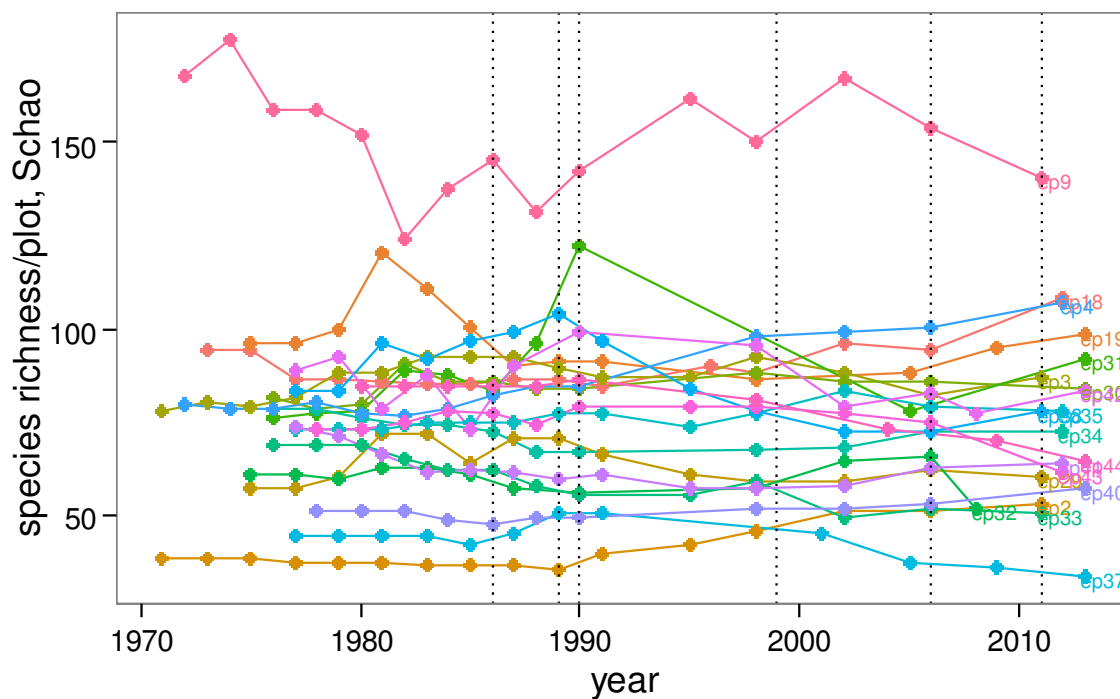


Figure 4.8 Value of Chao across plots. The Chao were almost constant with times in most of the plots

4.3.5 Effects of cyclones on effective number of common species

The effective number of common species (1D) in most of the forest plots were quiet consistent or having very slight changes in value across enumerated years (Figure 4.9). The GAM indicates that cyclones had no significant effects on 1D ($t = -1.16$, $p = 0.245$).

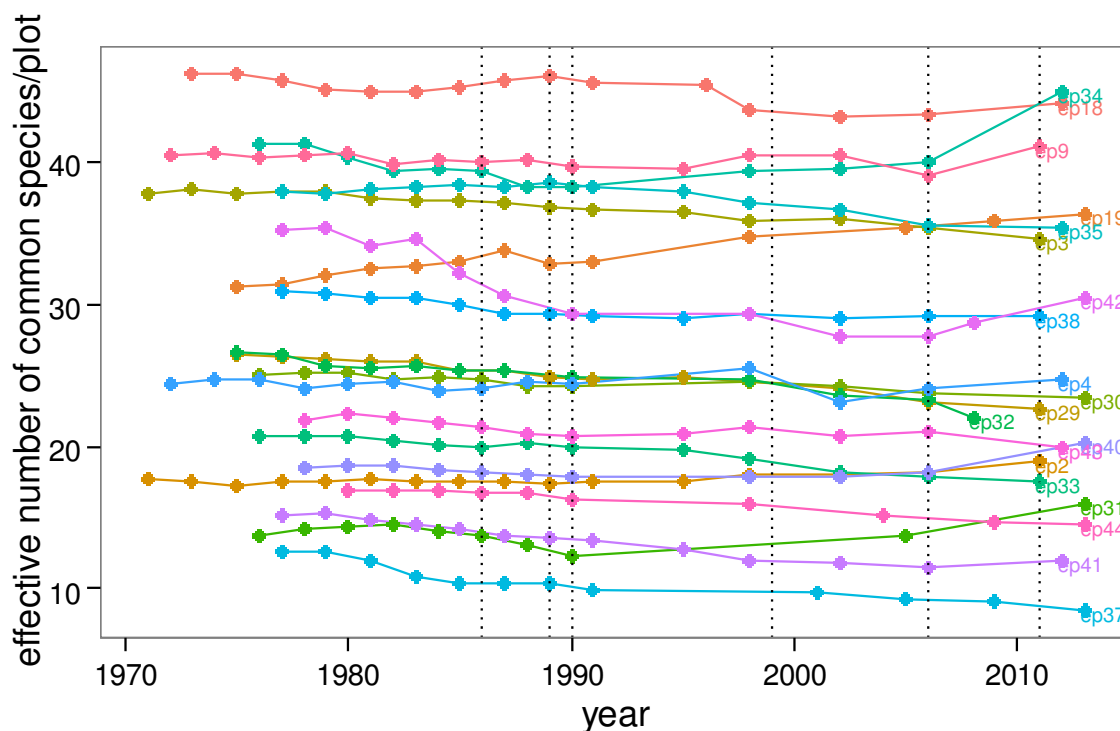


Figure 4.9 1D in each plot. Dotted vertical lines are cyclone event years

4.3.6 Effects of cyclones on effective number of abundant species, 2D

Small changes in effective number of abundant species (2D) can be seen between enumerated years in most of the plots (Figure 4.10), except for certain plots (EP42, EP37). On the whole, 2D decreased as indicated in the GAM plot (Figure 4.11). The model shows that there is a positive significant effect of cyclones on 2D ($t = 3.02$, $p = 0.003$), where around 0.121 ± 0.04 per plot 2D increase after each passage of cyclones on the plots.

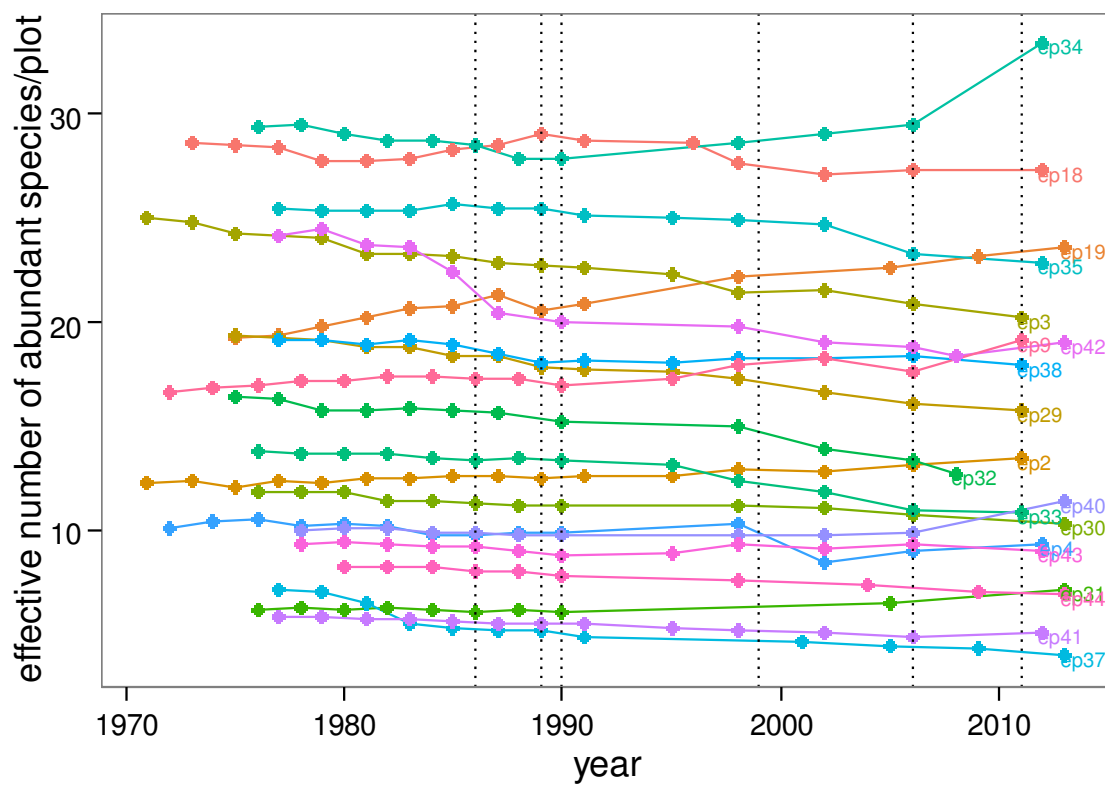


Figure 4.10 2D along years in each of the plots. Dotted vertical lines are cyclone event years

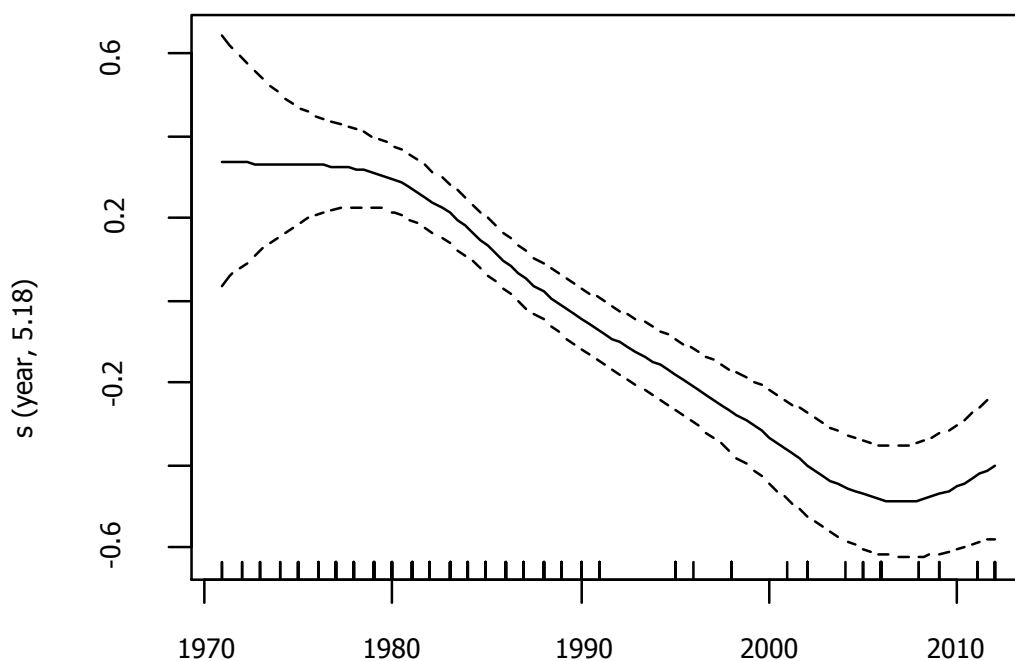


Figure 4.11 GAM plot shows smooth spline fit to time series of 2D since establishment of all plots with value of y-axis relative to time-averaged mean, under degree of freedom 5.18.

4.3.7 Effects of cyclones on stand level recruitment

Patterns of recruitment were distinctly different between each forest plot (Figure 4.12). The GAM indicates that the patterns in recruitment rates were not influenced by cyclone events ($p = 0.602$).

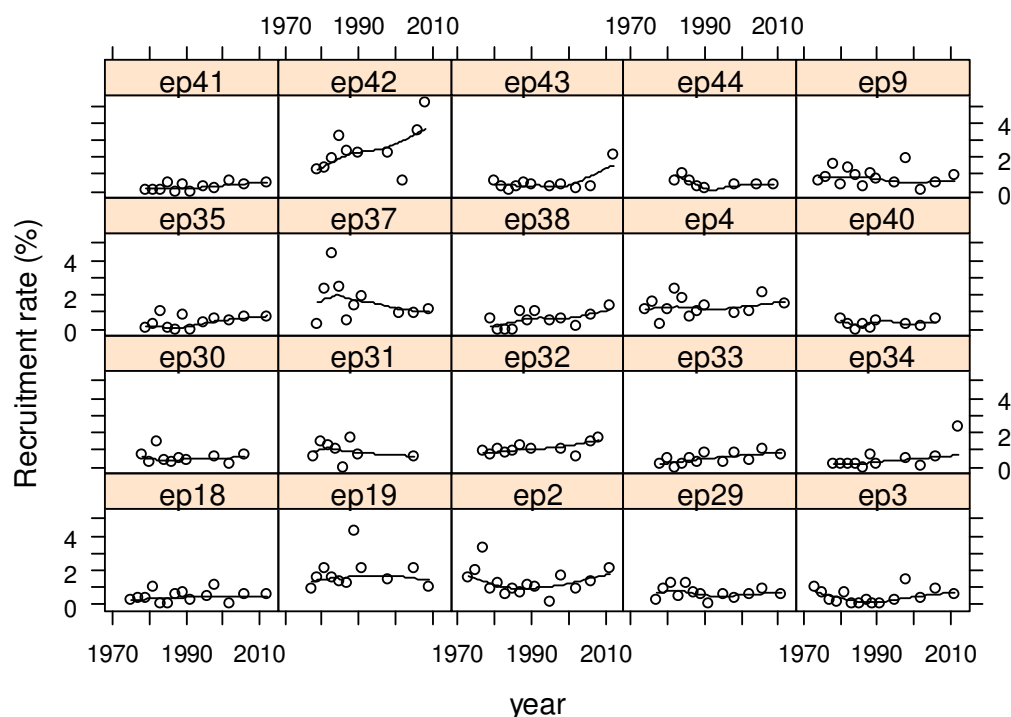


Figure 4.12 Percentages of recruitment in each of the plots using LOESS smoothing curve with span width of 0.75

4.3.8 Effects of cyclones on stand level mortality

There is a positive effect of cyclones in stand level mortality ($t = 6.249$, $p < 0.001$). The GAM for this variable estimated that for every passage of cyclones, death rate increased by $1.39 \pm 0.11\%$ per plot. The GAM plot (Figure 4.15) shows that mortality rates were increased from the 1990s, most probably due to series of cyclone events that occurred in the period of 1986 - 2011.

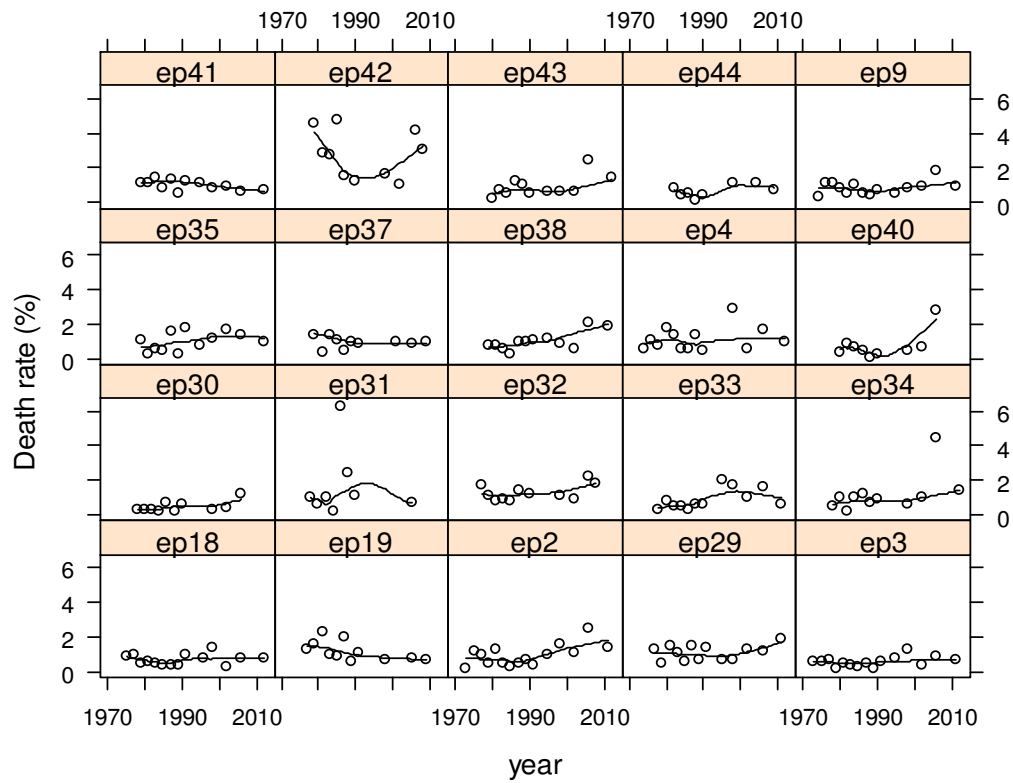


Figure 4.13 Percentages of mortality in each plots using LOESS smoothing curve with span width of 0.75

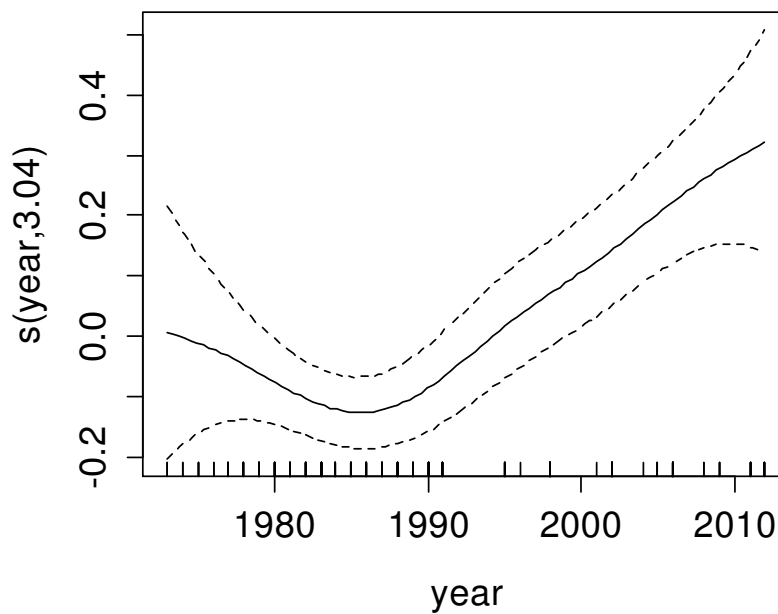


Figure 4.14 Smooth spline fit to time series on mortality rates of the 20 plots, with value of y-axis relative to time-averaged mean, under degree of freedom 3.04.

4.4 Discussion

As expected, total BA decreased following the cyclones. However, the effects of cyclones on total BA found in this study (reducing $0.703 \pm 0.08 \text{ m}^2 \text{ ha}^{-1}$) is relatively small for example if considering the range of total BA of $34.1 - 65.25 \text{ m}^2 \text{ ha}^{-1}$ before cyclone *Larry* take place in 2006 (Metcalf et al. 2008).

The increasing tree density following cyclones that was nearly significant is an unusual finding for the forests, since there is no evidence for long term increasing stem density (Murphy et al. 2013). Murphy even reported that stem density were decreased over the 40-year forest monitoring period. Similarly, their study considered the entire monitoring period as in the present study. Mean density change in their study was negative ($-0.27 \pm 0.68 \text{ stem} \geq 10 \text{ cm ha}^{-1}$) but cyclones were not mentioned as a factor. While the present study has shown that the stem density could be increased following a cyclone by $4.65 \pm 2.5 \text{ stem} \geq 10 \text{ cm ha}^{-1}$. The estimation of this cyclone effect is just near significant, but it provides a new insight because was unusual. One of the reasons could be because the present study emphasis is the direct effects of cyclone per plot. Whereas, the Murphy's study mainly accounted for patterns of tree density across all plots and years. Moreover, the increasing tree density following cyclones still could possibly happens, which has been found in other forests (De Gouvenain and Silander 2003).

In a study on cyclone-prone forests of Madagascar, number of trees increased following cyclones (De Gouvenain and Silander 2003). Higher tree density following cyclone was observed in African forests that experienced high tropical cyclone frequency (De Gouvenain and Silander 2003). In a study of lowland rain forests between New Guinea and Solomon Islands, the forests having higher stem densities and shorter canopies (Keppel et al. 2010). This could happen due to more light reaches saplings as canopy trees are damaged,

enhancing growth thus increasing the number of stems ≥ 10 cm dbh. In other cases, despite tree mortality increasing following a hurricane in Jamaica, more than half of trees (54 %) before the hurricane were still alive after the event (Tanner et al. 2014). The increased in stem density could also cause by the sapling of pioneer species that had reached required size for forest surveys, because enhanced by light exposure in forest gaps formed following the cyclones (Lewis and Bannar-Martin 2012). The repeated and frequent cyclones may therefore results in continuous existence of vegetation which characterised by shorter canopies and higher stem densities (De Gouvenain and Silander 2003, Keppel et al. 2010). Those studies may reflect a similar situation to the north Queensland forests that nearly has significant increase in stem density following cyclones.

Larger sized or higher canopy trees are normally exposed more to cyclones than intermediate or smaller trees may increase size inequalities. This study has found increasing trends over time in the Gini coefficient which means more unequal stem sizes. Gini has continuously increased since the 1970s, but with no obvious changes following cyclones in 1986 and 2006. A study by Curran et al. (2008a) also showed the same situation, where they found no sign that tree size influenced the type of cyclone damage to trees. Thus, as indicated by the GAM, cyclones are not the main cause of increasing inequality of tree size in the forest plots.

The higher effective number of abundant species following cyclones is an interesting finding for the forests in the present study, indicating that certain species more dominating following cyclone. Even though the effect was relatively small (0.121 ± 0.04 effective number of species per plot), the dominating species became slightly more abundant could be due to higher resistant towards cyclones. A study by Metcalfe et al. (2008) on the same forest area before cyclone *Larry* 2006 did not detect any significant difference in species richness of the affected plots and unaffected plots (60 ± 2.1 versus 58 ± 1.8), which means

species richness of the forests are quite stable. Similarly, this study also shows that the species density and number of common species in the forests were not significantly influenced by the cyclones. This finding is also similar to a lowland rain forests in the tropical South Pacific between New Guinea and Solomon Islands, where there is no effects of cyclone on species diversity (Keppel et al. 2010).

Even though cyclones did not significantly affect tree recruitment rates of the forests, it has been reported in other study that there were higher recruitments caused by extensive defoliation, loss of major branches and multiple tree falls following cyclone *Larry* in 2006 (Metcalf et al. 2008). A similar situation was found in other cyclone-prone rain forests, for example in Polynesia (Webb et al. 2011) and the Solomon Islands (Burslem et al. 2000) that found rapid recruitment after cyclones. Tree recruitment may also enhanced by light that reaches lower canopy trees (Bellingham et al. 1996) from tree gaps that created by tree death following cyclones. This situation may also contribute for the near significant increase in tree density found in this study.

The increased mortality rates is not an unusual phenomenon observed in the forests, since there was a high frequency of cyclones between 1986 and 2011 (two major cyclones - *Winifred* 1986 and *Larry* 2006, while the other four were minor) (Graham 2006). It is also a typical response when a forest experiencing strong cyclones (Webb et al. 2011, Webb et al. 2014). Changes in patterns of mortality rates with tree damage could be demonstrated by comparing patterns pre and post specific cyclone event (Cook and Goyens 2008, Tanner et al. 2014), or after a period of time (i.e., 2 years post cyclone) since mortality of trees maybe delayed (Zimmerman et al. 2014). In contrast with those studies, the present study describes the effects of cyclones regardless of any specific period of time or cyclone event. The nearly 1.5% increase in death rate per hectare following a cyclone found in this study is differently defined than mortality rates in other past studies on similar location. For example

Metcalfe and Bradford (2008) assessed dieback-affected area of the forests (not certainly mentioned whether caused by cyclones) which had an annual mortality rate of 9.20% compared to only 0.87% outside the affected area. Metcalfe et al. (2008) specifically compared mortality rates after cyclones between severe, moderate and slight damage sites which were 16.9-17.6%, 1.1-8.2% and <2% respectively. Murphy et al. (2008) concentrated on mortality rates of invasive species following cyclone *Larry* in 2006. These studies apparently emphasised mortality rates directed to the specific cyclone events and level of tree damage, while the present study presents provide insights in what is the direct effects of a cyclone across the long term mortality patterns of the forests.

Other studies also commonly found mortality increased following cyclones, but the studies were commonly based on changes in annual mortality rates pre and post cyclones. Hurricane Fran of North Carolina in 1996 has significantly increased 5 to 19 times higher than the annual percentage of death before the hurricane (Xi et al. 2008). Whereas in this study, the increase in mortality rates of 1.39 ± 0.11 % following cyclone would make up to 2 times higher than the original rates (range 0.2 – 1.37 % per year before cyclones). The larger effects of the Hurricane Fran maybe due to the annual mortality calculated from major tree species of the forests, while this thesis concerns on direct effects of cyclone. Similar to Hurricane Fran, Cyclone Olaf on the Polynesian island of Ta'u, American Samoa had 3 times larger annual mortality rates of cyclone-disturbed forest than undisturbed forest nearby (Webb et al. 2014). This study does not based on this comparison, but the 9 times larger annual mortality rates (Metcalfe et al. 2008) between cyclone disturbed forests than outside the affected areas is relatively higher than effects of Cyclone Olaf, or in range of the effects from Hurricane Fran.

Data and modelling constraints

The generalised additive modelling approach with whole stand data used here has high potential to provide information and understanding on cyclone effects due to the large dataset with multiple cyclones and many type of forest plot. While small data sets are prone to high sensitivity in model output. Even though the present study contained a reasonable long term data, it was found that the models would abruptly change in summary features even just by removing or adding data from a single measuring year.

Other uncertain factors that are not considered in the formulation of the models are also issues for the results. For example the 0.5 ha size of the plots is relatively small compared to the common size of plots in other studies. Thus, it is uncertain whether the variables measured within this plot size represent the responses or real situation of towards cyclones. In term of cyclone damage severity, some studies emphasised the magnitude of cyclone and relate them together. This factor could be one an important factor that should be accounted for this study, but was not able to be performed here due to incomplete information for each cyclone events (Curran et al. 2008a, Curran et al. 2008b, Metcalfe et al. 2008).

4.5 Conclusion

The models show that cyclones in tropical rain forests in the north Queensland significantly decrease total BA, increase the number of abundant species and increase tree mortality rates. In contrast, the cyclones not significantly affect tree size inequality, species density, number of common species, or tree recruitment rates. The stem density that was however nearly significantly increased could be due to more trees had reach the required size for forest survey (≥ 10 cm dbh) following cyclones.

The way this study describes the cyclone effects differs from other studies. Other studies commonly assess immediate impact after a specific cyclone event; or within a specific period; or in some cases by comparing pre cyclone and post cyclone patterns of the variables. In this study all data were used to obtain the effects of cyclones. The effects were presented as a numerical impact of a cyclone relative to the range of values possess by the variable. That means, this study highlights to what extent a variable within long term records was influenced by a single cyclone event.

The development of models in this study contributes some knowledge of the impacts of cyclones on the long term patterns of whole stand forest variables. The long term records of the variables not only demonstrate patterns with time, but also direct effects of cyclones. The smoothed overall pattern in each variable enables detection of whether the cyclones is a significant effect influencing the pattern.

The whole stand variables that were used in each model (i.e., the total BA, tree density, species diversity, mortality rates) are amongst the crucial attributes of the forest that may be influenced by large scale cyclones (Burslem et al. 2000, Baker et al. 2005). Even though the model that utilise the whole stand data could consider complexities not possible in other

approaches, still there are some gaps noticeable in the analyses. The whole stand variables that were used in each model (i.e., the total BA, tree density, species diversity, mortality rates) are amongst the crucial attributes of the forest that may be influenced by large scale cyclones (Burslem et al. 2000, Baker et al. 2005). For instance, in term of how cyclones affects individual trees. Hence more intensive modelling on individual tree data is required, which will be analysed in the next chapter on individual tree mortality and growth.

5 FACTORS AFFECTING INDIVIDUAL TREE MORTALITY AND TREE GROWTH ON THE TROPICAL RAIN FORESTS OF NORTH QUEENSLAND

5.1 Introduction

Individual mortality and growth of tropical rain forest trees are potentially influenced by forest disturbances (Hurst et al. 2012) and also intrinsic factors in the forest. Determining the effect of these factors is important to understand forest dynamics. As for the individual tree scale, studies of tree mortality and growth rate commonly emphasise the relationship between with stem sizes (Rüger et al. 2011, Iida et al. 2013), wood density (Curran et al. 2008b, Iida et al. 2012), family or species, or with forest disturbance (Burslem et al. 2000, Metcalfe et al. 2008). In North Queensland, with the 20 cases of plots experiencing cyclones (Graham 2006) from cyclones *Winifred* (1986), *Joy* (1990), *Rona* (1999) and *Larry* (2006), the cyclones may affect both mortality and growth of individual trees (Graham 2006, Metcalfe et al. 2008).

The importance of wood density for tree mortality and tree growth is widely recognised (Muller-Landau 2004, King et al. 2006, Chao et al. 2008, Sungpalee et al. 2009). High wood density trees are commonly observed to have an inverse relationship with both tree mortality and tree growth (Muller-Landau 2004, King et al. 2006, Chao et al. 2008, Sungpalee et al. 2009). Higher wood density trees are also believed to be less prone to death (Sungpalee et al. 2009) because of their higher wood strength (Chao et al. 2008, Larjavaara and Muller-Landau 2010). Low wood density is commonly found in fast growing species, suggesting taxonomic background should also be considered as an important factor influencing tree mortality or tree growth. Therefore it is crucial to determine the effect of wood density on tree growth and mortality.

The relationship among neighbouring trees could also influence tree growth and likelihood of death. Crowding effects in local area of a tree would create competition among individuals for space or basal area, soil nutrients, water or light resources. The tree competition could affects growth rates, which may also influenced by stem size (Ostertag et al. 2005) or the crown volume (Fraver et al. 2014). Since competition could lead the growth rates of trees to increase, therefore it is important to understand the crowding effect of the tree and possible relationships to the stem size for example.

Objectives of study

The current chapter aims to quantify the effects of variables linked to individual tree mortality and growth by analysing them in a modelling approach. The mortality model utilised logistic regression of binomial data on status (dead and alive) of individual trees, while the growth model used continuous data of basal area growth rates of each tree. The general objective of this study is to determine individual and stand level variables that influence individual tree mortality and tree growth and their relative importance.

The specific hypotheses for the tree death model are assigned based on literature and common ecological principles:

1. Tree death is less likely higher wood density
2. Trees with low growth rates are more likely to die
3. Trees with higher crowding effects of basal area or tree density are more likely to die
4. Trees are more likely to die in cyclones

The specific hypotheses for the tree growth rate model are:

1. Growth rates are expected to be lower with higher wood density trees
2. Higher crowding effects of basal area and density are likely to decrease growth rates
3. Growth rates will be higher following cyclones

4. Crowding effects of basal area are likely to decrease the growth rates for larger basal area size of focal trees
5. Cyclones are likely to increase the growth rates when wood density is higher

5.2 Methodology

5.2.1 Sources of data

The data for this chapter were prepared by incorporating available parameters from the CSIRO dataset and newly derived data (Table 5.1). The available parameters were records of cyclones, taxonomic levels (family, genus or species), wood density and diameter at breast height. Other potential parameters were basal area, growth rates and indexes of crowding effects or neighbourhood competition index. Candidate variables for both models are listed in Table 5.1.

Table 5.1 Variables in the CSIRO dataset used as candidate for mortality or growth factors.

	Individual level parameters:	Stand level parameters:
<i>Available data</i>	<ul style="list-style-type: none"> • Family/genus/species • Diameter at breast height (dbh) • Wood density (WD) 	<ul style="list-style-type: none"> • Cyclones
<i>Derived data</i>	<ul style="list-style-type: none"> • Basal area (BA) • Growth rates: <ul style="list-style-type: none"> – growth rate of BA in m² per year (BAGR) • Neighbourhood competition indexes (NCI): <ul style="list-style-type: none"> – NCI of tree density (NCI.dens) – NCI of BA (NCI.BA) – NCI of species density (NCI.SR) 	

Neighbourhood competition indices (NCI) or crowding effects were prepared to identify the extent to which survival or growth of each tree is influenced by the competitive effects of neighbours. NCI was calculated using *markstat* in R *spatstat* package (Baddeley and Turner 2005) by obtaining the total value of a variable (i.e., tree density, basal area or species density) for all available trees ≥ 10 cm dbh within 5 m, excluding the value of the focal tree

(Figure 5.1) and correcting for plot edge effects. NCIs prepared in this study were NCI of tree density, NCI of basal area and NCI of species density (SR).

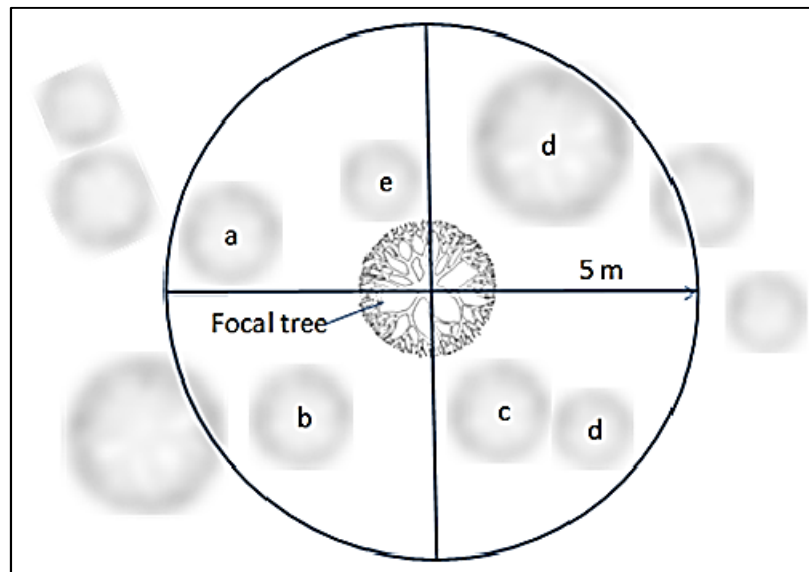


Figure 5.1 The NCIs prepared by summing up the total value (e.g. BA) for each potential neighbourhood tree in 5 m radius (i.e. $a+b+c+d+e+r^{\text{th}}$ tree) excluding value of the focal tree.

Some minor exclusions of tree data were made from the dataset. The first tree measurements and first year of establishment in every plot were excluded since there was no data on mortality and growth rates. In some cases certain tree measurements were omitted since their dbh mark had been raised during the subsequent survey, which could lead to data errors. Several measurements considered as outliers were also removed from the data. Some tree measurements are considered irregular as they were far from the general growth pattern. The irregular tree measurement consist of 58 trees which apparently had shrunk in dbh more than 20 mm yr^{-1} or grown more than 30 mm yr^{-1} . The final data contained about 90% of the original data following the filtration process.

5.2.2 Development of the mortality model

All possible factors affecting tree mortality were initially grouped (Table 5.2) to reduce collinearity problem among factors with similar features. Only one variable from the growth-related and one from sized-related group were selected since other group members represent similar attributes. In the *Other variables* group, all variables were used in the model since there were no signs of collinearity during model inspection. There are two parameters selected from the *Taxon related* group which are WD and Family. WD was kept in numerical format, while families were treated as a factor.

The explanatory variable of growth rates (GR) were factorised in the model into two groups: trees with normal growth rates and trees with negative growth rates. The family Rutaceae was arranged as the control family due to the mortality rate of the family being close to the average mortality rate across families. Moreover, Rutaceae is a common family in the study site and exists at relatively high tree density.

Some interactions between variable were also assigned for the model as there could be more complex relationships affecting individual tree mortality, such as interactions between wood densities of trees with the cyclone events or between the crowding effects and tree size. The high or low wood density trees may die differently during cyclone or no cyclone. Crowding effects may be dependent on the relative sizes of trees.

The analysis used generalised linear mixed modelling (GLMM) with the *lme4* package (Bates et al. 2014) in R 3.1.1 (R Development Core Team 2014). Plot and year of survey were set as random effects. The model assigned probability of each tree death as a binomial response variable.

Table 5.2 Possible factors influencing tree mortality. Abbreviation used in this table similar with Table 5.1

Group of variable	Related parameters
<i>Taxon related</i>	WD, Family, Genus, Species
<i>Tree-size related</i>	BA
<i>Tree-growth related</i> (unit per year ⁻¹)	GR
<i>Other variables</i>	Cyclones, NCI.dens, NCI.BA
<i>Interaction</i> (: symbol)	NCI.BA : BA WD : Cyclones
<i>Random effects</i>	Plot, year

The full model of tree mortality consists of explanatory variable comprising two representative from the *Taxon related* group (WD and Family) and from *Other variables* group (NCI.dens and NCI.BA); one from *Tree-size related* group (BA) and *Tree-growth related* group (GR); two types of *Interaction* and the random effects (plot and year) as briefly described in Table 5.3. The full model was given by:

$$\begin{aligned} \text{Probability of tree death} = & \\ & \text{WD} + \text{GR} + \text{BA} + \text{NCI.BA} + \text{NCI.dens} + \text{Cyclones} + \text{NCI.BA} : \text{BA} \\ & + \text{WD} : \text{Cyclones} + \text{GR} : \text{Cyclones} + \text{Family} + 1|\text{plot/year} \end{aligned}$$

Table 5.3 Description of variables used in the mortality model

Variable	Description
Probability of death	The response variable (0 = Alive, 1 = Dead)
GR	Factorised growth rate (1= negative growth rate, 2 = normal growth)
WD	Wood density of each species for each tree
Family	Family for each individual tree. The baseline family is the Rutaceae
NCI.BA	Neighbourhood competition index in BA
NCI.dens	Neighbourhood competition index in tree density
Cyclones	Cyclone in the survey year (Y = Yes, N = No)

NCI.BA:BA	BAGR might depend on the interaction between BA and the crowding effects of BA (NCI)
WD:cyclones	BAGR might depend on wood density in the year with cyclone/no cyclone
plot/year	Random effects of plot and year

The model was then simplified based on AIC to obtain the minimum adequate model. The final model provides estimates of how each variable influences the probability of tree mortality. A summary of the model fit was used to identify the strength of the relationships. Odd ratios were generated for the mortality model to determine whether the factors increase or decrease the probability of death. The odds ratios were log-transformed for clearer evaluations, quantified from the intercept as relative change in probability of death per unit variable. Background information on prominent families fits by the models was also obtained (Hyland et al. 2003).

5.2.3 The growth model

The growth model used LME (Linear Mixed Effects) under R package *nlme* (Pinheiro et al. 2014) . Plot and year of survey were set as random effects. BAGR in the unit of $\text{m}^2 \text{yr}^{-1}$ was chosen as the response variable. The family Proteaceae was used as the control family in the model since the average BA growth rate of the family was close to the average growth rate across families. Moreover, the family is a common family in the study site with relatively high tree density. The model assigned the BA growth rates as the continuous response variable, which were modelled as a function of the selected explanatory variables in Table 5.4. The full growth model equation is given by:

Individual tree basal area growth, BAGR ($\text{m}^2 \text{year}^{-1}$) =
WD + Family+ NCI.BA + NCI.dens + cyclones + NCI.BA:BA + WD:cyclones,
random = $\sim 1|\text{plot/year}$

Table 5.4 Possible factors influencing individual tree growth of the tropical rain forests

Variable	Description
BAGR	Continuous response variable of basal area growth rate in m ² per year
WD	Wood density of each species for each tree
Family	Family for each individual tree. The baseline family is the Proteaceae
NCI.BA	Neighbourhood competition index in BA
NCI.dens	Neighbourhood competition index in tree density
Cyclones	Cyclone in the survey year (Y = Yes, N = No)
NCI.BA:BA	BAGR might depend on the interaction between BA and the crowding effects of BA (NCI)
WD:cyclones	BAGR might depend on wood density in the year with cyclone/no cyclone
plot/year	Random effects of plot and year

5.3 Results

5.3.1 Mortality analysis

From the final mortality model, the odds ratio for the intercept was 0.03, indicating around 3% of overall tree death per year. The model discovered three significant variables: negative growth rates, wood density and family (with twenty two significant families) that make up twenty four factors influencing tree death (Table 5.5). This means, trees that shrink, low wood density or in certain families are more likely to die.

The final model is given by:

$$\text{Mortality status} = \text{WD} + \text{negative GR} + \text{Family} + 1|\text{plot/year}$$

Table 5.5 Summary of the final mortality model. Factors with odds ratio of more than 1 indicate increased chances of death relative to the intercept, while odds ratio of less than 1 decreased.

	Estimate	Standard Error	P value	Odds ratio	Odds ratio limit		Relative percentage per servay
					Lower	upper	
Intercept	-3.41	0.16	<0.001	0.03	0.02	0.05	3.0
Variables:							
Negative growth rates	1.41	0.06	<0.001	4.09	3.64	4.59	12.3
Wood density (g cm ⁻³)	-0.85	0.2	<0.001	0.43	0.29	0.63	1.29
Family:							
Winteraceae	1.2	0.37	<0.01	3.31	1.59	6.88	9.93
Symplocaceae	1.02	0.25	<0.001	2.78	1.7	4.55	8.34
Thymelaeaceae	0.99	0.31	<0.01	2.70	1.48	4.93	8.1
Grossulariaceae	0.82	0.22	<0.001	2.26	1.46	3.5	6.78
Eupomatiaceae	0.7	0.32	<0.05	2.01	1.06	3.79	6.03
Araliaceae	0.69	0.15	<0.001	2.00	1.5	2.66	6.0
Myrsinaceae	0.56	0.24	<0.05	1.75	1.08	2.83	5.25
Sapindaceae	0.41	0.12	<0.01	1.50	1.18	1.92	4.5
Mimosaceae	0.34	0.16	<0.05	1.40	1.04	1.9	4.2

Myrtaceae	-0.39	0.1	<0.001	0.67	0.55	0.83	2.01
Myristicaceae	-0.47	0.2	<0.05	0.62	0.42	0.93	1.86
Aquifoliaceae	-0.55	0.28	<0.05	0.57	0.33	0.99	1.71
Flacourtiaceae	-0.56	0.27	<0.05	0.57	0.34	0.97	1.71
Xanthophyllaceae	-0.82	0.26	<0.01	0.44	0.27	0.73	1.32
Arecaceae	-0.83	0.13	<0.001	0.44	0.34	0.57	1.32
Cunoniaceae	-0.86	0.2	<0.001	0.42	0.29	0.63	1.26
Fabaceae	-0.87	0.34	<0.01	0.42	0.22	0.81	1.26
Anacardiaceae	-0.94	0.46	<0.05	0.39	0.16	0.97	1.17
Celastraceae	-1.24	0.52	<0.05	0.29	0.11	0.8	0.87
Nyctaginaceae	-1.39	0.37	<0.001	0.25	0.12	0.51	0.75
Idiospermaceae	-1.73	0.72	<0.05	0.18	0.04	0.73	0.54
Araucariaceae	-2.13	0.72	<0.01	0.12	0.03	0.49	0.36

There are ten positive factors (log odds ratio > 0), while the other fourteen are negative factors (log odds ratio < 0). The probability of tree death is likely to be increased with negative growth rate of trees (in mm per year) and for trees from any member of the families Winteraceae, Symplocaceae, Thymelaeaceae, Grossulariaceae, Eupomatiaceae, Araliaceae, Myrsinaceae, Sapindaceae and Mimosaceae. In contrast, probability of tree death is likely reduced by increased wood density and for members of thirteen families: Myrtaceae, Myristicaceae, Aquifoliaceae, Flacourtiaceae, Xanthophyllaceae, Arecaceae, Cunoniaceae, Fabaceae, Anacardiaceae, Celastraceae, Nyctaginaceae, Idiospermaceae or Araucariaceae. The odds ratios of the significant factors were log-transformed to aid visual interpretation (Figure 5.3). Visual inspection of residuals plotted from the model did not reveal any obvious deviations from normality.

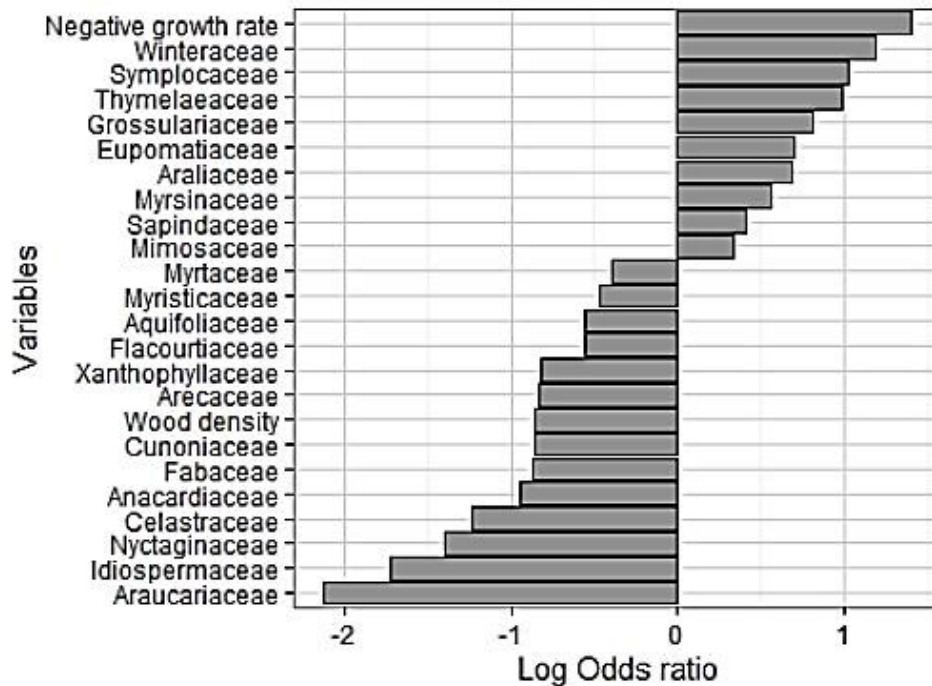


Figure 5.2 Log odds ratio for the twenty four significant factors of tree mortality. Variable with log odds ratio > 0 are likely to increase the tree mortality rate while log odds ratio < 0 are likely to reduce the tree mortality rate.

The model indicates that for a negative growth rate tree, the probability of death increases to 12.3% (odds ratio*overall death rate). Figure 5.4 clearly shows that trees with negative growth rates have higher probability of death, however the negative growth rates trees are likely to have very small effects on the forest plots since they occur at relatively low tree density compared to positive growth rate trees (Figure 5.5).

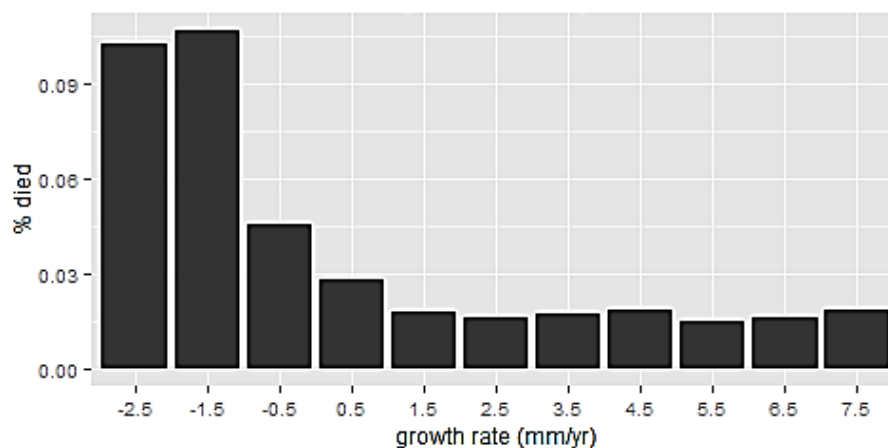


Figure 5.3 Histograms of tree growth rates and death percentage across all trees

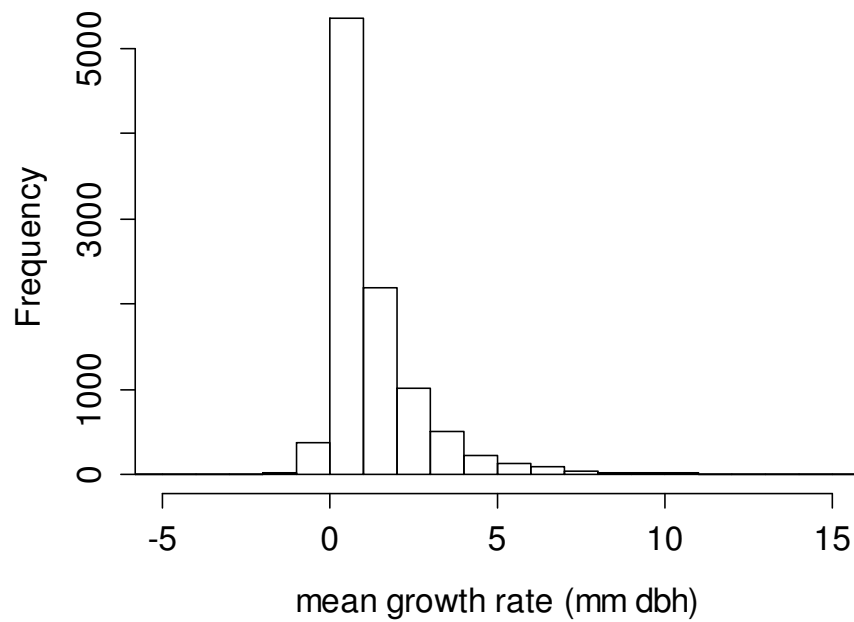


Figure 5.4 Histogram of average growth rate across years of individual tree in the plots (using breaks = 30)

Higher wood density reduces chances of tree death to 1.3 % for every additional 1 g cm^{-3} . Given that the range of wood density is between 0.16 g cm^{-3} to 1.04 g cm^{-3} with average wood density of 0.61 g cm^{-3} (Figure 5.6), the effect of this variable on observed death rates could be relatively small. Nonetheless, low wood density trees (below average $\sim 0.6 \text{ g cm}^{-3}$) have relatively higher death rates (Figure 5.7).

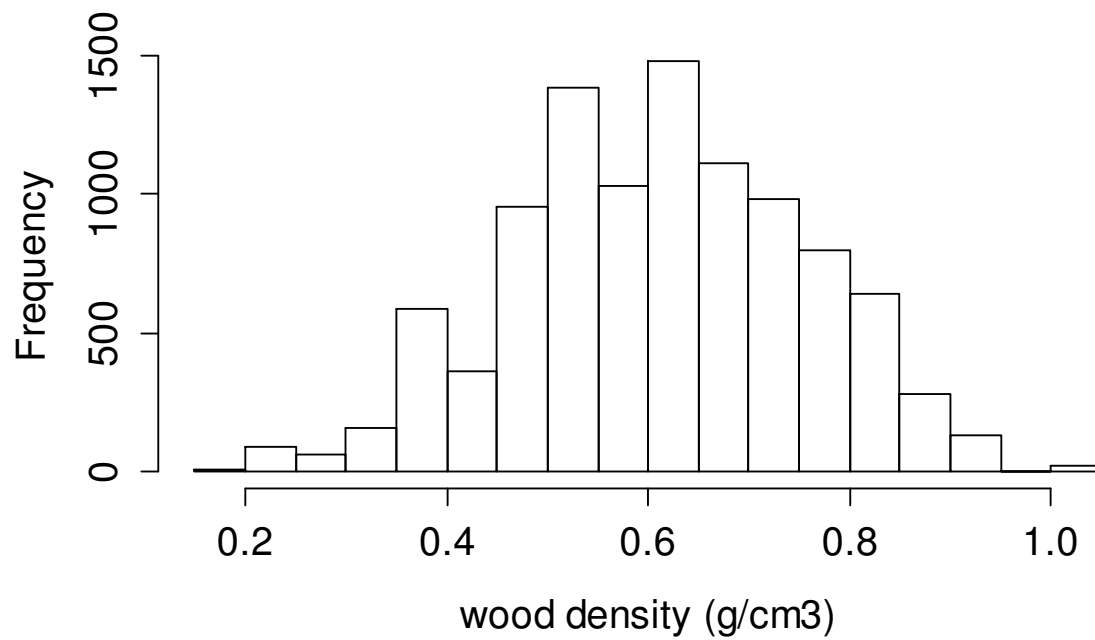


Figure 5.5 Range of wood density and frequency of individual trees (using breaks = 20)

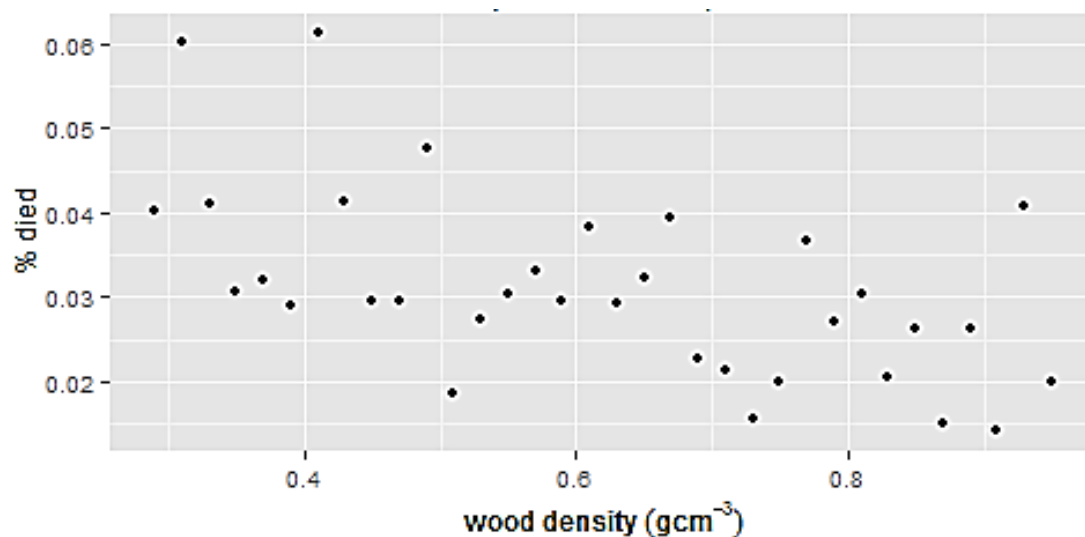


Figure 5.6 Percentages of death rate across wood density of the individual trees ≥ 10 cm dbh of the forest plots

The influence of each positive and negative family factor on the mortality rate was determined based on the multiplication of the annual mortality rate with the odds ratio, summarised in Table 5.6.

Table 5.6 Influence of family factors on mortality rates relative to Rutaceae

Family	Change in death probability (%)	Number of individual	Family	Change in death probability (%)	Number of individual
Winteraceae	+ 9.93	16	Nyctaginaceae	- 0.75	43
Symplocaceae	+ 8.34	38	Celastraceae	- 0.87	42
Thymelaeaceae	+ 8.10	22	Anacardiaceae	- 1.17	28
Grossulariaceae	+ 6.78	59	Fabaceae	- 1.26	71
Eupomatiaceae	+ 6.03	27	Cunoniaceae	- 1.26	304
Araliaceae	+ 6.00	177	Arecaceae	- 1.32	545
Myrsinaceae	+ 5.25	53	Xanthophyllaceae	- 1.32	107
Sapindaceae	+ 4.50	283	Flacourtiaceae	- 1.71	70
Mimosaceae	+ 4.20	149	Aquifoliaceae	- 1.71	73
Araucariaceae	- 0.36	52	Myristicaceae	- 1.86	138
Idiospermaceae	- 0.54	28	Myrtaceae	- 2.01	1025

Percentage of tree death in cyclone years was higher than cyclone-free years (Figure 5.8). However, cyclones are not a significant factor influencing the overall mortality rate. This could be because the number of tree observations during cyclone years are fewer than those when no cyclone occurs (Figure 5.9). Other candidate influencing factors like crowding effects (NCIs) and interactions were also not significant.

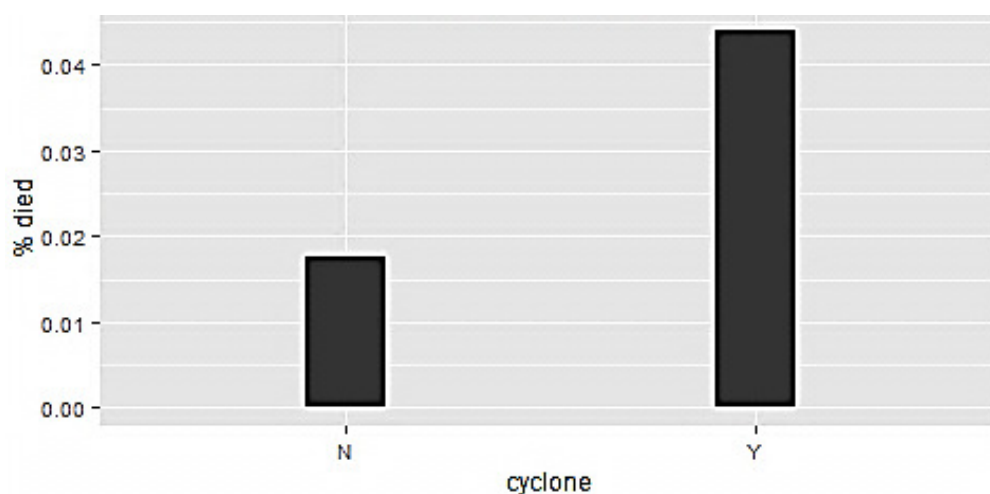


Figure 5.7 Percentage of individual trees over alive trees in no cyclone years and trees died over alive trees in cyclone years, across all plots and years (N = No cyclone, Y = Cyclone occurs)''

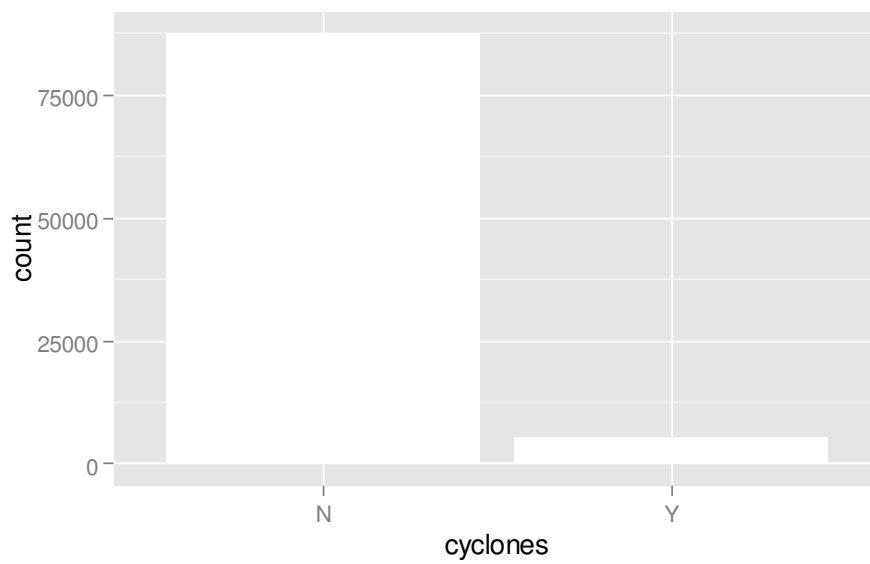


Figure 5.8 Cyclones experiences based on all observation in each trees across all plots and years (count = number of observations)

5.3.2 Growth analysis

From the model, wood density, crowding effects of BA, crowding effects of density, cyclones, interactions and more than half of the seventy families are significant factors influencing the basal area growth rates of trees (Table 5.7).

Table 5.7 Summary of the growth model

Variables	value	std.error	t.value	p.value
cyclones	1.97	0.66	2.98	0.0029
Wood density	-3.19	0.36	-8.98	<0.001
Wood density:cyclones	-3.17	1.06	-2.99	0.0027
NCI.BA	-2.94	0.13	-22.05	<0.001
NCI.BA:BA	41.16	0.24	169.46	<0.001
NCI.dens	0.05	0.01	3.77	0.0002
Families:				
Combretaceae	10.13	2.26	4.48	<0.001
Himantandraceae	-18.38	1.70	-10.80	<0.001
Araucariaceae	8.01	0.50	16.04	<0.001
Xanthophyllaceae	-2.96	0.37	-8.02	<0.001
Anacardiaceae	6.45	0.65	9.98	<0.001
Aquifoliaceae	-3.77	0.42	-9.02	<0.001
Myrtaceae	-1.11	0.21	-5.36	<0.001
Burseraceae	-3.41	0.49	-6.97	<0.001
Arecaceae	-3.61	0.25	-14.40	<0.001
Rutaceae	1.13	0.19	5.98	<0.001
Rubiaceae	-1.78	0.27	-6.60	<0.001
Fabaceae	-2.58	0.58	-4.48	<0.001
Icacinaceae	-2.70	0.29	-9.45	<0.001
Sterculiaceae	1.67	0.23	7.40	<0.001
Myristicaceae	-2.61	0.40	-6.57	<0.001
Datiscaceae	50.93	2.00	25.49	<0.001
Nyctaginaceae	-6.83	0.74	-9.20	<0.001
Elaeocarpaceae	3.77	0.25	15.18	<0.001
Meliaceae	2.44	0.37	6.57	<0.001
Rhamnaceae	2.02	0.43	4.73	<0.001
Urticaceae	-5.37	0.46	-11.65	<0.001
Euphorbiaceae	-1.62	0.22	-7.34	<0.001
Monimiaceae	-3.84	0.3	-12.90	<0.001
Eupomatiaceae	-3.86	0.79	-4.91	<0.001
Araliaceae	-1.57	0.37	-4.30	<0.001
Simaroubaceae	-5.08	1.31	-3.87	<0.001

Zamiaceae	-5.20	1.37	-3.79	<0.001
Podocarpaceae	-3.15	0.83	-3.77	<0.001
Balanopaceae	2.35	0.65	3.62	<0.001
Flacourtiaceae	-1.62	0.44	-3.65	<0.001
Lamiaceae	-5.55	1.55	-3.57	<0.001
Ochnaceae	-1.20	0.34	-3.50	<0.001
Thymelaeaceae	-2.56	0.75	-3.42	<0.001
Celastraceae	-1.98	0.59	-3.35	<0.001
Idiospermaceae	2.10	0.65	3.22	0.001
Winteraceae	-3.74	1.17	-3.20	0.001
Theaceae	-3.99	1.34	-2.97	0.003
Lecythidaceae	-7.59	2.79	-2.72	0.006
Oleaceae	-1.39	0.52	-2.65	0.008
Grossulariaceae	-1.31	0.52	-2.54	0.011
Violaceae	-9.90	4.08	-2.42	0.015
Ebenaceae	-1.56	0.65	-2.41	0.015
Sapotaceae	-0.69	0.29	-2.36	0.018
Apocynaceae	-0.94	0.4	-2.35	0.019
Sapindaceae	-0.62	0.28	-2.24	0.025
Myrsinaceae	-1.09	0.5	-2.17	0.03
Tiliaceae	7.15	3.6	1.98	0.05

The average basal area growth rate of trees is $0.000604 \text{ m}^2 \text{ yr}^{-1}$ across all trees in period from 1973 to 2012. The model indicates that occurrence of a cyclone increases basal area growth rates. Mean basal area growth rate for trees that experienced a cyclone was relatively higher with huge difference compared to no-cyclone experience trees, which is $0.00062 \text{ m}^2 \text{ yr}^{-1}$ and $0.000588 \text{ m}^2 \text{ yr}^{-1}$ respectively.

Average basal area growth rates vary with wood density. Most trees have average growth rate of less than $0.001 \text{ m}^2 \text{ yr}^{-1}$ (Figure 5.9). The model shows that trees with higher wood density are likely to have lower growth rates. Furthermore, the growth rates and wood density relationship also depends on the occurrence of cyclones. Within similar wood density scale, trees growth rates is likely to be lower in the presence of cyclone compared to the one with no cyclone experience (p value = 0.0027).

Growth rates decrease for higher crowding effects of basal area. But if the focal trees are larger, the effects were reverse with increases in growth rates. Higher crowding effects of tree density in local area also found increases the growth rates.

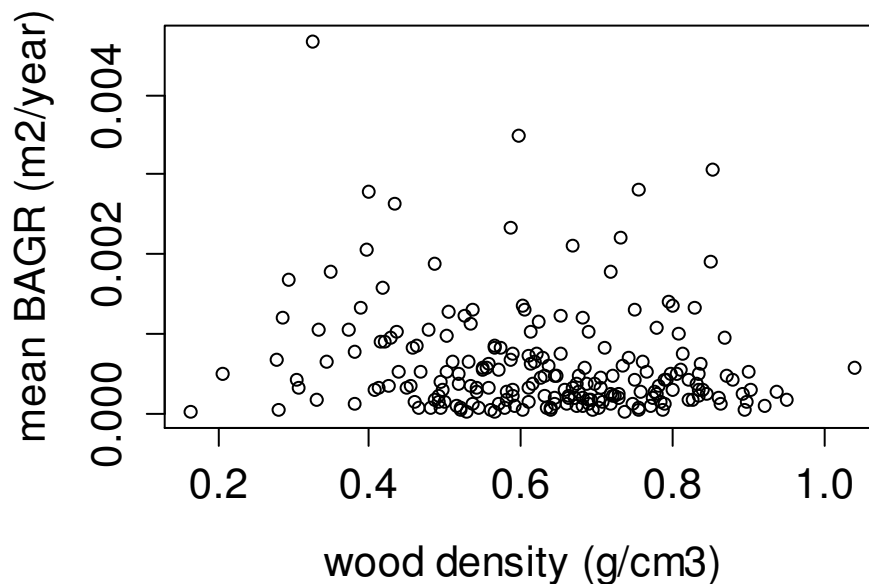


Figure 5.9 Average basal area growth rates across all individual trees grouped by the range of wood density

Basal area growth rates may also depend on family. From the model, more than half of the families significantly increase or decrease the basal area growth rates relative to Protaceae. Most of the significant families influenced the growth rate negatively, for example the most prominent families are Himantandraceae and Violaceae. Other families influenced for higher growth rates like Combretaceae and Datisceae. When looking at the number of trees of these prominent effect families, they make up a small number of trees in the forest (Table 5.8). In contrast, Rutaceae may also influence the plot level growth since they exist in a large number of trees.

Table 5.8 Other details of some significant families in influencing the basal area growth rates

Family	Number of existing trees across all plots
Combretaceae	2
Datiscaceae	5
Himantandraceae	4
Rutaceae	1298
Violaceae	1

5.4 Discussion

5.4.1 Factors affecting individual tree mortality

The 3.01% of average annual mortality rate of this study is relatively low compared to the 7.9% annual mortality rate in cyclone-prone forests on Polynesian islands (Webb et al. 2014). The range of mortality rate from 1.2 to 9.2% is larger than the mortality range of 1.4 to 2.2% per year for > 4.9 cm DBH trees in Kolombangara, Solomon Islands (Burslem et al. 2000). The maximum 9 % mortality rate is still higher than the 7% six-month mortality rates interval immediately after cyclones in the Kolombangara, which are similar to the Polynesian annual mortality rates. Though the mortality percentages were lower than Webb's (2014) study, they were much higher than Burslem et al. (2000) study. Compared to both of the cyclones-prone forests of Polynesia and Solomon Islands, the North Queensland tropical forests can be considered to have intermediate tree mortality rates.

The mortality rates along years for most of the forest plots were quite consistent prior to the first recorded cyclone in 1986 except for several plots, but after that the mortality rates changed to almost 2% or more in many of the plots. The prominent increasing death rates in 1986 and 2006 are perhaps due to the widespread damage observed (Metcalf et al. 2008) most probably caused by the major cyclones *Winifred* (1986) and *Larry* (2006). However, the model has found that the cyclones are not a significant influence for overall mortality rates. This might be due to the frequent and less damaging storms experienced by the forests. The major cyclones are actually only cyclone *Winifred* (1986) which involved 5 plots and cyclone *Larry* (2006) that involved ten plots. Minor cyclonic winds in 1980 involved one plot, cyclone *Joy* (1990) only affected one plot and cyclone *Rona* (1999) two plots.

Trees with negative growth rate have almost four times higher death probability than growing trees. However, the effects on mortality rates may be small since only around 5 % of all trees recorded with negative growth rate.

The model also indicates wood density to be one of the significant factors affecting probability of tree death. Higher wood density trees were less likely to die, similar with findings in many studies (Muller-Landau 2004, King et al. 2006, Chao et al. 2008, Sungpalee et al. 2009, Iida et al. 2012, Lewis and Bannar-Martin 2012, Aubry-Kientz et al. 2013). In Barro Colorado Island (Muller-Landau 2004), trees of ≥ 10 cm show the same pattern of decreasing tree mortality with higher wood density, but a relatively smaller range than in North Queensland. The death rate for lowest wood density trees ($\sim 0.3 \text{ g cm}^{-3}$) in Barro Colorado Island was around 0.02%, whereas in the North Queensland forests 0.02 % mortality rates was held by among highest wood density tree ($\sim 0.8 \text{ g cm}^{-3}$ and $\sim 0.95 \text{ g cm}^{-3}$ trees). This indicates lower wood density trees in North Queensland would have much higher probability than trees with similar wood density in Barro Colorado Island. When comparing the high wood density trees in North Queensland ($> 0.8 \text{ g cm}^{-3}$) with trees that possess 1 g cm^{-3} wood density in Pasoh and Lambir (King et al. 2006), trees in North Queensland had a slightly higher death rates ($\sim 0.01\%$ in Pasoh and Lambir). The difference in death rates per tree wood density used in Barro Colorado Island, Pasoh and Lambir may not be important for this comparison because the North Queensland forests are very different forests though, yet still showing the common relationship where mortality decrease with higher wood density forest trees.

In term of the family traits, most of the positive family factors are small trees like Sapindaceae, vines or single-stemmed like Araliaceae, or commonly shrubby or understory trees like Symplocaceae. They influence individual mortality rates, but in term of tree numbers they are scarce within the study area. For example only 16 trees of Winteraceae

were ever recorded in the plots, 22 trees from Thymelaceae and 27 trees of Eupomaceae from around ten thousand trees. Negative factor families like the Myrtaceae have relatively in small negative effects on the mortality rates, but they are abundant (1025 trees).

5.4.2 Factors affecting tree growth rates

The significant negative relationship of growth rates with higher wood density is generally consistent with other studies in tropical rain forests, such as in Panama (Muller-Landau 2004), Peninsular Malaysia (King et al. 2005) and Amazon (Chao et al. 2008). Within a certain wood density, growth rate of trees facing cyclone were also found to have lower growth than no cyclone trees. As expected, occurrence of cyclone increased the growth rates. The average growth rates of cyclone-experienced trees is around 5% higher than non-cyclone experienced trees can be considered as a very huge difference, indicating cyclone as a crucial factor in influencing the growth rates. Therefore, cyclones occurrence relatively important in growth rates besides wood density.

Higher crowding effects of basal area decreasing the growth rates most probably because allocation of plant sources such as mineral, water and lights were distributed more to support larger total basal areas. The more distributed the sources, the less total sources receive by individual trees thus decreasing the growth rates. But this effects are depends on the size of the focal trees. In contrast, reverse effects will occur if focal trees are larger than other trees of the local area, forcing the smaller surrounding trees to grow faster to compete for light sources. This study has found the interaction between crowding effect of total basal area with basal area size has relatively higher impact on growth rates compared to crowding effects of the basal area alone. This indicates tree sizes are important contribution to the growth rates. Effects of higher crowding effects of tree density indicates additional trees would increase the growth rates, which may be triggered by competition among trees for

light sources. However, the model indicates that the impact of crowding effects of tree density on the growth rates are very low.

More than half of the available families in the forests are factors influencing the growth rates. Prominent families that increase the growth rates like Combretaceae and Datisceae are found in certain plots, but relatively in low density across all plots. The Combretaceae consist only species *Terminalia sericocarpa*. The increased effects on growth rates from this family may be related to the nature of the species which is leafless for a period during September of October (Boland et al. 2006). However, to date no data available or no evidence found to show that the period causing higher tree growth. Trees from this family found in a very low density across all plots. Same situation also observed in the family Datisceae, where only four trees of species *Tetrameles nudiflora* were recorded across all plots. Decreasing effects families also have very low density of individual trees, which are only four trees of *Galbulimima baccata* from Himantandraceae and one tree of *Rinorea bengalensis* from Violaceae exist. Due to the low tree densities and small number of species within these prominent families, it can be concluded that they may be not so importantly affecting the growth rates across all forests.

5.5 Conclusion

In chapter 3 and 4 of this thesis, cyclones have been observed to have significant effects on tree mortality seen through spatial pattern and stand level analysis of the forests. The current chapter works on the individual level data of the forest trees. It can be clearly seen that the cyclones influenced individual growth rates of the forest trees but not the individual tree mortality rates. Other factors such as wood density and crowding effects of trees were found to influence both individual tree growth and tree death.

The mortality model

From the analysis, this study revealed that chance of death is higher for a tree that has lower wood density, negative growth rates and belongs to a particular set of families. In contrast, high wood density, positive growth rates or certain other families are less prone to death. One of the most remarkable results noticed from the mortality model is cyclones have no significant effect on individual tree mortality rates. The factors influencing individual mortality rates found here may only be applicable for trees in this particular region.

The growth model

The model indicates that growth rates of individual trees increase when there are higher crowding effects of tree density, occurrence of cyclone, crowding effects from larger focal tree size and trees from some families. In contrast, growth rates decrease when wood density of the individual trees is higher; there are higher crowding effects of tree basal area; and for trees from other families. Based on this varying effects scale, factors influencing growth rates can be considered as complex.

6 DISCUSSION AND CONCLUSION

The research questions addressed in this thesis were:

- 1) Do cyclones affect stem distribution, spatial patterns and tree interactions in the forests?
- 2) How do cyclones impact on stand level properties (total basal area, stem density, stem size inequality, species diversity, mortality rates and recruitment rates) of the forests?
- 3) How do tree individual factors influence mortality rates and growth rates? Do cyclones have an impact on individual tree mortality and growth rates?

There were 20 records of cyclone across all of the forests plots. This study generally predicted that the disturbances would trigger the tree community of the forests to change in spatial pattern, stand level properties and individual tree properties in response to the cyclones. As cyclones can lead to forest structural adaptation for cyclones towards forest resilience (Lugo 2008), patterns of structural change caused by cyclones in this study had similar relationships to those recorded in several cyclone-prone tropical forests.

Cyclones have minor effects on spatial patterns of the forests and not affecting tree size distribution

Main findings from this study include that cyclones can be seen to affect the physical spatial patterns of the trees, tree basal area and tree deaths. The changes are restricted to certain years in certain plots. The finding from this initial analysis of the thesis indicates that cyclones cause differences in tree mortality, recruitment and growth across trees, years and plots. Stem density and basal area decreased following cyclones. Even though the analysis was done as a graphic snapshot comparison, in terms of percentage reduction the changes

is lower than those reported in a cyclone prone forest for example in Mona island, Mexico (42% reduction in stem density, 25.4% in basal area, Rojas-Sandoval et al. (2014)).

The test for interaction between trees found very minor evidence of tree segregation or clustering (the pair correlation function, PCF test) or size dependency based on the tree locations (mark correlation function, MCF test). The PCF test found very small scale changes in spatial patterns influenced by cyclones during cyclone *Winifred* (significant spatial patterns only found in one plot out of five affected plots), cyclone *Larry* (found only in two plots out ten affected plots), no significant influence at all following cyclone *Rona*, *Joy* and other cyclonic winds. The MCF test found no significant patterns at all across all cyclone events. These findings may be caused by several possibilities:

- i. The trees less likely depends on distance between pair of trees thus small scale tree clustering is only found at distances of less than 5 m
- ii. There may be possibilities of clustering further than the maximum estimation of spatial pattern that was possible for the plots (only up to 12 m) as in many studies (up to 50 m, also based on plot size)
- iii. The forests may be very stable even though facing frequent cyclones

Even though the graphical snapshot comparison of the spatial pattern maps were much less reliable than tree interaction analyses, the spatial analysis chapter shown that the graphical comparison study had at least provides some baseline information and background on the cyclone effects as a basis for other analyses in the subsequent chapters. Information obtained from the changes in Gini prior to the cyclone events has also shown the approach is crucial to explain the forest changes. Like in a study done by Coomes and Allen (2007b), tree size inequality were traced and combine with description of spatial patterns to understand effects of forest competitive thinning and disturbance.

Inequality in stem size (Gini coefficient) that assessed though trends had shown size inequality prominently increased across years in most plots, however cyclones apparently not the factors influencing the trends. Somehow, the study of Gini trends indicates that the increasing size inequality as a sign of forest growth.

A cyclone event may increase or decrease the stand level forest properties

The stand level analysis found an occurrence of cyclone directly affects some stand level properties of the forests which are:

- i. decreasing the total BA
- ii. increasing number of abundant species
- iii. increasing tree mortality rates
- iv. may increase stem density

The direct effects were detailed up to the numerical effects from cyclone in increasing or decreasing the stand level properties. The cyclone effect obtained in this study were just estimations, but provides new insights since it is very rare to find direct effects of cyclone being discussed in the literature that assess a long term forest survey with frequent cyclone events.

A variety of individual factors affect tree death and growth

The stand level analysis found that cyclone significantly affect the growth rates. However, cyclones were not a significant factor on individual mortality rates. This could be due to the differences in modelling approach conducted for analysing the stand level properties and the individual level properties

Other key findings for this chapter are:

- i. Higher wood density trees able to survive better following cyclones. The high wood density trees may be structurally stronger
- ii. Higher wood density trees has slower growth rate than the lower wood density trees following cyclones.
- iii. Trees with negative growth rates in at least a part of their life are more likely to die
- iv. Crowding effects influences both individual tree mortality and tree growth. Higher crowding generally reduces both rates.

Summary of the key findings

Forests that experienced cyclones even once have different features to those with no cyclone experience. However, even when compared with other cyclone prone forests from different tropical region, this study found that the overall influence of cyclones on North Queensland rain forests is apparently less prominent. Several reasons for this could be because of the resilience or cyclone-adaptive strategy of the forests, or by the time limiting factor after cyclones to see the explicit effects of cyclones.

The cyclone-prone forests could be adapted to the frequent disturbances of the forests where individual trees may built a resistance strategy towards cyclones (Plotkin et al. 2012), while forests that rarely face cyclones may receive relatively higher damage magnitudes. Nevertheless, the strategies for facing cyclones may vary by forest type and tree communities. The findings are supported by several studies in other forests, for example, denser forests and shorter canopies (although the current study not precisely measure canopy height) of forests following repeated and frequent cyclone occurrence (De Goudenain and Silander 2003, Keppel et al. 2010).

Limitations of the research

This analysis is based on extensive record of forest surveys. Accordingly the data may reflect collecting errors. For example during field surveys, estimation of stem coordinates had inaccuracies to the extent of 1 metre. This technical limitation considerably influenced the outcome of this study, especially for the spatial pattern analysis which is quite sensitive to spatial errors.

The size of the plot also plays an important role. The forest plot size of 0.5 ha is relatively very small compared with the common plot size of other long term studies, which can be at least 9 ha (Picard et al. 2009) or as large as 50 ha as in common size for Center for Tropical Forest Science network plots (Condit et al. 2014). A large plot size provides higher possibilities to trace or analyse any changes for example in the spatial pattern. Even though number of trees in most of the plots is adequate for analysis, due to the limited plot size, the sensitivity of analysis is reduced. Due to this limitation, precise interactions between tree marks and pattern of trees in the forest are less likely to be obtained, because commonly this type of analysis requires a relatively larger plot to reveal changes in spatial patterns.

Changes in spatial patterns and significant factors affected by cyclones were quite difficult to trace graphically or in modelling approach. It may be because too immediate survey years were used. Even though the calculation of growth, recruitment and mortality rates used offset, but lack other option available instead of using the immediate surveyed year. In most of the plots, years assessed for post cyclone responses were taken on the nearest surveyed year before and after cyclone events. This situation takes place especially in affected plots after cyclone *Larry* and *Winifred*. The year 2006 was used in almost all plots affected by cyclone *Larry*, immediately after the cyclone in March 2006. There was only one affected plot not surveyed in 2006 but resurveyed in 2013, however the dbh data for 2013 were

incomplete. 1986 was used to assess changes in spatial patterns after cyclone *Winifred* in most of the affected plots, which occurred just a few months before the forest survey.

Generally, effects of cyclones are best detected 10 - 20 years after the event. After that the effects decrease slowly (De Gouvenain and Silander 2003). But 10 – 20 years are actually still considered as immediate responses according to Lugo (2008). The earliest cyclone-affected forests studied in this chapter were forests that experienced cyclones since 1986, which are > 20 years of records. However, other cyclone events in most of the plots can be considered as causing short-term or immediate effects (0 to 3 years) (Lugo 2008). For instance, the period after the cyclone in 2006 could be considered as a very recent one and the effects may not be an ideal duration for studying the immediate responses of cyclones.

Overall, the data serves may not be long enough to see the changes after cyclones. Compared to other studies, the assessment always take place in years longer after the cyclone, thus the trees have enough time for recovery making subsequent changes of the spatial patterns more assessable to study. Otherwise, the immediate years of assessment of this chapter still provides quite consistent results with tree damages after cyclone *Larry* (Metcalf et al. 2008).

For the modelling analyses in this study, even though the data used were from long term monitoring, most of the period after cyclone events studied in this thesis also considered as the immediate direct effects of cyclones. Perhaps longer time duration of studies is needed for the forests (Murphy et al. 2008) to appraise the effects of cyclones.

For the qualitative assessment of the map visualisation, there may also be biases in evaluation. Most of the outcomes are in contrast with the result of pair and mark correlation function and the trend in total BA. But since both approaches of map visualisation and

statistical measures have different objectives, the results were presented separately in the chapter.

Recommendations and conclusion

The results of this study support the hypothesis that cyclones will lead to considerable changes in forest structure. Nevertheless, the cyclone-adaptation mechanisms that lead to forests resilience in North Queensland appear to be more complex relative to other tropical rain forests, which may be determined with longer term monitoring following cyclones. The influence of the cyclones on the forest structure can be considered relatively low and not very prominent compare to the magnitude of damage faced by other forests experiencing cyclones. For example cyclones had not significant effects on individual tree mortality. The spatial pattern analysis (chapter 3) seemed to not explicitly support the hypothesis that forest structure on North Queensland is primarily cyclone-driven. The effects of cyclones on individual tree mortality was also negative as analysed by the model in Chapter 5. But the stand level model (chapter 4) showed that cyclones influence most stand level parameters, perhaps most importantly suggesting that the cyclones influence the dynamics of the tree communities and individual tree growth, but not individual tree mortality.

From another perspective, the individual trees that are not influenced by cyclones could be related to the adaptation of the trees towards the frequent cyclone, which may also due to the biogeographical characteristics and uniqueness of the North Queensland forests. However there is no evidence that these are the main reasons that influence the ability of the forest to resist the disturbances. These differences may also depend on the time scale of the data being studied. Ultimately, acquiring effects of disturbances from the cyclones may require longer term studies with regards to the uniqueness of the North Queensland tropical rain forests. One of the scenarios that could arise from the unique biogeography is in terms

of tree communities, which may be becoming more resistant to cyclones effects and to cyclone-driven mortality, cyclone-driven recruitment or cyclone-driven growth (Murphy et al. 2013).

Forest resilience in this area may have also changed, given that the forest resilience post-cyclone may takes longer than in other tropical rain forests, as reported by Murphy et al. (2013). Thus, there may be other perspectives that could be worth exploring for understanding cyclone effects, such as analysing the forest-cyclones response based on biogeographic relationships, strength or class of the cyclones or investigating phylogenetic background of the forest trees. The data set used here has shown the impacts of cyclones on the stand level and individual trees specifically for the forests of North Queensland, Australia. This study should be extended in the future, maybe by considering a longer term after cyclone events, investigating relationships of the cyclone effects with biogeographical features of the area or understanding individual tree physical responses on cyclone passages through the forests.

In conclusion, the results from this research suggest that although the overall effect of cyclones on North Queensland tropical rain forests are generally less prominent than cyclone prone forests in other tropic regions, there is variations in the dynamics of the North Queensland tropical rain forests that provide insights. The stem distribution, spatial patterns and tree interactions of the forests is less likely influenced by the cyclones. Cyclone is a factor increasing the stand level mortality but no evidence found in affecting individual mortality. Some families are important in influencing the individual mortality and growth rates. Nevertheless, the dynamics of the forest tree communities from individual trees characters of mortality and growth, trends in spatial patterns and influences in the stand level has characterised the tropical rain forests of North Queensland for facing the frequent cyclones.

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